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New species of *Labiobaetis* Novikova & Kluge from New Guinea (Ephemeroptera, Baetidae): a never-ending story of diversity

Thomas Kaltenbach[1,2], Laurent Vuataz[1,2], Jean-Luc Gattolliat[1,2]

1 *Muséum cantonal des Sciences Naturelles, Département de zoologie, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland*

2 *University of Lausanne (UNIL), Department of Ecology and Evolution, CH-1015 Lausanne, Switzerland*

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Corresponding author: Thomas Kaltenbach (thomas.kaltenbach@bluewin.ch)

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Abstract

Investigations of material collected partly in 1999 and mainly between 2006 and 2016 in New Guinea, mostly along the high, central mountain chain of the island, further increased our knowledge of the diversity of the genus *Labiobaetis* Novikova & Kluge on this island. Previously, 37 species were reported from New Guinea. We have identified six new species using a combination of morphology and genetic analysis (COI). They are described and illustrated based on their larvae. Five of the six new species belong to the group *petersorum*, which is endemic to the island. Additionally, *Labiobaetis xeniolus* Lugo-Ortiz & McCafferty is also assigned to this group. The morphological characterisation of the group *petersorum* is enhanced, and a key to all species of this group is provided. Complementary descriptions and remarks to the morphology of known species of the group *petersorum* are provided. Additionally, a genetic analysis (COI) including most species and several additional Molecular Operational Taxonomic Units (MOTUs) of the group *petersorum* is discussed. One of the new species belongs to the group *vitilis*. The morphological characterization of this group is slightly enhanced, and the obtained COI sequence was added to the genetic analysis of the group *petersorum*. The total number of *Labiobaetis* species worldwide is augmented to 162.

Key Words

COI, integrative taxonomy, mayflies, morphology, MOTU

Introduction

The genus *Labiobaetis* Novikova & Kluge, 1987 is part of the Baetidae, which is the most divers family of Ephemeroptera, including approximately one third of all mayfly species worldwide (> 1160 species) in ca. 118 genera (Sartori and Brittain 2015; Jacobus et al. 2019; updated by the authors). *Labiobaetis* is the most divers genus of Baetidae and one of the most divers amongst mayflies in general, with 156 previously described species (Barber-James et al. 2013; Kaltenbach and Gattolliat 2018, 2019, 2020, 2021 and citations therein; Kaltenbach et al. 2020, 2022a and citations therein). The distribution of *Labiobaetis* is nearly worldwide, except for the Neotropical realm, New Zealand, New Caledonia and some remote islands. The history and concept of *Labiobaetis* were summarized in detail by Shi and Tong (2014) and Kaltenbach and Gattolliat (2018).

This contribution will focus on further new species of *Labiobaetis* from New Guinea. The first six species of *Labiobaetis* from New Guinea were reported by Lugo-Ortiz et al. (1999). Subsequently, a large study was carried out by Kaltenbach and Gattolliat (2018) with the description of 26 new species, followed by two smaller studies with additional new species (Kaltenbach et al. 2021a; Kaltenbach and Gattolliat 2021). Presently, a total of 37 species of *Labiobaetis* are reported from New Guinea. Six additional species are described in this study, augmenting the total number for New Guinea to 43 species, which is the highest density of different species worldwide for this genus. Five of the new species belong to the group *petersorum*, erected in Kaltenbach and Gattolliat (2018),

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which is the focus in this study. The morphological definition of the group is enhanced, another already known species was added (*L. xeniolus* Lugo-Ortiz & McCafferty, 1999), and COI sequences of the group are analysed. One of the new species belongs to the group *vitilis*, erected in Kaltenbach and Gattolliat (2018). The morphological characterization of the group is slightly enhanced, and the obtained COI sequence was added to the genetic analysis of the group *petersorum*.

New Guinea, the second largest island after Greenland, is known for its exceptional diversity. It is a geological composite consisting of many separate terranes; the evolutionary history of the biota involves connections to the Australian landmass, uplift, volcanism, and rifting that accompanied the tectonic events (Allison 2010). There is strong evidence that recent environmental change in the extremely structured central highlands of New Guinea with its ongoing formation of rich aquatic resources, remote valleys and mountain blocks has been the primary driver of diversification of aquatic insects in that area (Toussaint et al. 2013, 2014).

Given the extraordinary diversity of New Guinea, the limited collection efforts in the past, the presence of many unexplored areas, and the exceptional richness of *Labiobaetis* on the island, it is reasonable to anticipate the discovery of numerous additional species through future collection efforts.

Materials and methods

All specimens were preserved in 70%–96% ethanol. The dissection of larvae was done in Cellosolve (2-Ethoxyethanol) with subsequent mounting on slides with Euparal liquid, using an Olympus SZX7 stereomicroscope.

Photographs of larvae were taken using a Canon EOS 6D camera and processed with the programs Adobe Photoshop Lightroom (http://www.adobe.com) and Helicon Focus version 5.3 (http://www.heliconsoft.com). Photographs of larval parts on slides were taken with an Olympus BX43 microscope equipped with an Olympus SC 50 camera and the program Olympus CellSense v. 4.1. The SEM picture was taken using a FEI Quanta FEC 250 electron microscope (Thermo Fisher). All photographs were subsequently enhanced with Adobe Photoshop Elements 13.

The DNA of part of the specimens was extracted using non-destructive methods allowing subsequent morphological analysis (see Vuataz et al. 2011 for details). We amplified a 658 bp fragment of the mitochondrial gene cytochrome oxidase subunit 1 (COI) using the primers LCO 1490 and HCO 2198 (Folmer et al. 1994, see Kaltenbach and Gattolliat 2020 for details). Sequencing was done with Sanger's method (Sanger et al. 1977). Forward and reverse sequencing reads were assembled and edited in CodonCode Aligner 10.0.2 (Codon-Code Corporation, Dedham, MA), and aligned using MAFFT (Katoh et al. 2019) with default settings as implemented in Jalview 2.11.2.6 (Waterhouse et al. 2009). The number of parsimony-informative sites of the alignment was calculated in MegaX (Kumar et al. 2018; Stecher et al. 2020). Pairwise COI distances were calculated using the dist.dna function of the ape 5.7-1 package (Paradis and Schliep 2019) for R 4.2.3 (R Core Team 2023), under the raw model and the pairwise.deletion option, corresponding to uncorrected p-distances (see Srivathsan and Meier 2012) with missing data removed in a pairwise way. Mean, minimum and maximum distances within and between COI putative species, referred to as Molecular Operational Taxonomic Units hereafter (MOTUs), were calculated using the ddply function of the plyr 1.8.8 package (Wickham 2011). The COI sequences were attributed to species based on morphological evidence, with seven additional MOTUs within *L.* cf. *xeniolus* (*L.* cf. *xeniolus* A–G) defined according to the most conservative species delimitation method (i.e., GMYC; see below).

Before reconstructing the COI gene tree, the best evolutionary model (GTR+ Γ +I) was estimated following the second-order Akaike information criterion (AICc; Hurvich and Tsai 1989) implemented in JModelTest 2.1.10 (Darriba et al 2012) with five substitution schemes and six Γ categories and all other parameters set to default. To accommodate different substitution rates among COI codon positions, we analysed our data set in two partitions, one with first and second codon positions and one with third positions (1 + 2, 3). Bayesian inference (BI) gene tree reconstruction was conducted in MrBayes 3.2.7a (Ronquist et al. 2012). Two independent analyses of four MCMC chains run for three million generations with trees sampled every 1'000 generations were implemented, and the first 10% of generations were discarded as burn-in after visually verifying run stationarity and convergence in Tracer 1.7.2 (Rambaut et al. 2018). The sequence GBIFCH00975629, corresponding to *L. kokoda* sp. nov. (Table 1), was used as outgroup as it is the only non-member of the group *petersorum* (see Results). The consensus tree was visualized and edited in iTOL 6.7.4 (Letunic and Bork 2021).

To explore COI evolutionary divergence and compare it to our morphological identifications, we applied three single-locus species delimitation methods to our COI data set: the distance-based ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2020), the tree-based PTP (Poisson Tree Processes; Zhang et al 2013) and GMYC (General Mixed Yule-Coalescent; Pons et al. 2006; Fujisawa and Barraclough 2013) approaches. The ASAP method, which is an improvement of the widely used ABGD (Automatic Barcode Gap Discovery; Puillandre et al. 2012) approach, has the advantage of providing a score (i.e., asap-score) that designates the most likely number of hypothetical species. The PTP approach exploits the differences between the relationships among and within species, using the number of substitutions from a phylogenetic tree. The GMYC model, which also exploits intra and interspecies phylogenetic differences, uses time rather than direct number of substitutions, and thus requires a time-calibrated ultrametric tree as input. ASAP was applied to our COI alignment using the ASAP web-

server available at https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html, computing the genetic distances under simple p-distances with all other settings set to default. Input maximum likelihood tree for PTP was generated in RAxML-NG 1.1.0 (Kozlov et al. 2019) from our COI alignment, selecting the all-in-one (ML search + bootstrapping) option and MRE-based bootstrap convergence criterion. The best model of evolution and the partition scheme specified above, as well as 50 random and 50 parsimony starting trees were implemented. PTP was conducted on the web service available at https://mptp.h-its.org, selecting the partition with the lowest asap-score. Input BI ultra-metric tree for GMYC was generated in BEAST 1.10.4. (Suchard et al. 2018). To avoid potential biases in threshold estimation, the identical COI haplotypes were pruned (see Talavera et al. 2013) using Collapsetypes 4.6 (Chesters 2013). Input BEAST file was created in BEAUTi 1.10.4 (Suchard et al. 2018), implementing the best model of evolution and the partition scheme specified above, and selecting a relaxed molecular clock (uncorrelated lognormal) model, a coalescent (constant size) prior (see Monaghan et al. 2009) and a UPGMA starting tree. Two independent MCMC chains were run for 30 million generations, sampling trees every 1000 generations. Run stationarity and convergence was visually verified in Tracer and the independent log and tree files were combined using LogCombiner 1.10.4 (Suchard et al. 2018) after discarding the first 10% of the trees as burn-in. The maximum clade credibility tree, generated in TreeAnnotator 1.10.4 (Suchard et al. 2018) with all options set to default, was used as input for GMYC, which was run in R using the SPLITS package 1.0-20 (Ezard et al. 2021). We favoured the single-threshold version of the GMYC model because it was shown to outperform the multiple-threshold version (Fujisawa and Barraclough 2013).

The GenBank accession numbers are given in Table 1, nomenclature of gene sequences follows Chakrabarty et al. (2013).

The distribution maps were generated with the program SimpleMappr (https://simplemappr.net, Shorthouse 2010).

The dichotomous keys were elaborated with the support of the program DKey v. 1.3.0 (http://drawwing.org/dkey, Tofilski 2018).

The terminology follows Hubbard (1995), Kluge (2004) and Kluge 2005 (term "protopteron"). The term "blank" is used to describe an unpigmented area of cuticle (Kluge et al. 2023).

Table 1. Sequenced specimens.

Species	Specimen voucher catalogue #	GenBank # (COI)	GenSeq Nomenclature
L. gladius	GBIFCH00465179	MH619486	genseq-4 COI
L. janae	GBIFCH00465181	MH619483	genseq-1 COI
	GBIFCH00465182	MH619489	genseq-2 COI
L. amber sp. nov.	GBIFCH00763716	OQ947296	genseq-2 COI
L. bilibil sp. nov.	GBIFCH00763602	OQ947297	genseq-2 COI
L. kinibeli sp. nov.	GBIFCH00829887	OQ947310	genseq-2 COI
	GBIFCH00975628	OQ947311	genseq-1 COI
	GBIFCH00975632	OQ947312	genseq-2 COI
	GBIFCH00763775	OQ947309	genseq-2 COI
L. nabire sp. nov.	GBIFCH00980888	OQ947313	genseq-1 COI
	GBIFCH00980889	OQ947314	genseq-2 COI
L. cf. *petersorum*	GBIFCH00763702	OQ955856	genseq-4 COI
L. cf. *xeniolus* A	GBIFCH00829891	OQ947299	genseq-4 COI
	GBIFCH00829892	OQ947300	genseq-4 COI
	GBIFCH00829890	OQ947298	genseq-4 COI
L. cf. *xeniolus* B	GBIFCH00829889	OQ947302	genseq-4 COI
	GBIFCH00829888	OQ947301	genseq-4 COI
L. cf. *xeniolus* C	GBIFCH00763703	OQ947303	genseq-4 COI
L. cf. *xeniolus* D	GBIFCH00975631	OQ947304	genseq-4 COI
L. cf. *xeniolus* E	GBIFCH00975627	OQ947305	genseq-4 COI
L. cf. *xeniolus* F	GBIFCH00763704	OQ947306	genseq-4 COI
	GBIFCH00975630	OQ947307	genseq-4 COI
L. cf. *xeniolus* G	GBIFCH00829894	OQ947308	genseq-4 COI
L. sp. 1	GBIFCH00763711	OQ947315	genseq-4 COI
L. kokoda sp. nov.	GBIFCH00975629	OQ947316	genseq-1 COI

Results

New species descriptions

Abbreviations:

MZB Museum Zoologicum Bogoriense (Indonesia);
MZL Muséum cantonal des Sciences Naturelles, Lausanne (Switzerland);
ZSM Zoologische Staatssammlung München (Germany).

List of *Labiobaetis* species treated in this paper

petersorum group

1. *L. petersorum* (Lugo-Ortiz & McCafferty, 1999)
2. *L. xeniolus* (Lugo-Ortiz & McCafferty, 1999)
3. *L. gladius* Kaltenbach & Gattolliat, 2018
4. *L. janae* Kaltenbach & Gattolliat, 2018
5. *L. amber* sp. nov.
6. *L. bilibil* sp. nov.
7. *L. kinibeli* sp. nov.
8. *L. nabire* sp. nov.
9. *L. simbuensis* sp. nov.

vitilis group

10. *L. kokoda* sp. nov.

Labiobaetis petersorum group of species
(diagnosis enhanced from Kaltenbach and Gattolliat 2018)

Following combination of characters: A) antennal scape without distolateral process; antennal pedicel distally with triangular scales; flagellum usually with dots in middle part (Fig. 6a, b); B) labrum sub-rectangular, wide; dorsal, submarginal arc of setae well developed, composed of long, simple setae (Fig. 2a, b); C) both mandibles with outermost denticle blade-like enlarged (Fig. 9c, d, f, g); D) hy-

popharynx apically with well-developed tuft of stout setae, distolaterally with two additional tufts of setae; superlinguae distolaterally protruding (Fig. 3a); E) maxillary palp segment II distally pointed, constricted (Fig. 3c); F) labial palp segment II with thumb-like distomedial protuberance, apically rounded (Fig. 4d); G) hind protoptera absent; H) femur wide; dorsal margin with numerous short to medium, spine-like setae (usually > 40); apex on posterior side with stout setae on fore and middle leg, not on hind leg (Fig. 5a, e); I) claw with convex ventral margin; with long, fine, subapical seta in anterior position (between apex and first denticle. Subapical setae fine and transparent, sometimes difficult to see; seems to break easily and may also stick to the claw) (Fig. 12j, k); J) tergalii present on segments II–VII; usually large, tracheae strongly pigmented; anal margin with both long and short setae (Fig. 13d, e).

The *L. petersorum* group is known from New Guinea only, including the following species:

Labiobaetis petersorum
Labiobaetis xeniolus (new assignment to the group)
Labiobaetis gladius
Labiobaetis janae
Labiobaetis amber sp. nov.
Labiobaetis bilibil sp. nov.
Labiobaetis kinibeli sp. nov.
Labiobaetis nabire sp. nov.
Labiobaetis simbuensis sp. nov.

1. *Labiobaetis petersorum* (Lugo-Ortiz & McCafferty, 1999)

Pseudocloeon petersorum: Lugo-Ortiz et al. 1999.
Labiobaetis petersorum: Kaltenbach and Gattolliat 2018: fig. 16a–d.

Remarks to morphology. Larva. Based on the original description and the figures in Lugo-Ortiz et al. 1999, most of the diagnostic characters of group *petersorum* are present. Exceptions are: the presence of dots on the flagellum; two additional distolateral tufts of setae on hypopharynx; stout setae on posterior apex of fore and middle legs; anal margin of the tergalii with both short and long setae. These characters remain unknown until reexamination of type material. Subapical setae are also not described for this species.

Labiobaetis cf. *petersorum*: we studied specimens morphologically very similar to *L. petersorum*, but collected in a location far away from the type locality of *L. petersorum* (Fig. 38a, b). Unfortunately, we cannot compare COI sequences, because of the lack of a sequence from the type locality or nearby. Because of the geographical distance, we prefer to remain prudent and denominate these specimens as "cf. *petersorum*". Interestingly, they have all characters of the group *petersorum*, except subapical setae.

Material examined (*L.* cf. *petersorum*). INDONESIA • 7 larvae; Papua Barat, Tamrau, Mts N of Kebar, sandy sunny riverbank; 00°47'02"S, 133°04'20"E; 758 m; 07.xi.2013; leg. M. Balke; (BH032); 1 on slide; GBIFCH00763702; 6 in alcohol; GBIFCH00975710; MZL.

2. *Labiobaetis xeniolus* (Lugo-Ortiz & McCafferty, 1999)

Pseudocloeon xeniolum: Lugo-Ortiz et al. 1999.

Remarks to morphology. Larva. Based on the original description and the figures in Lugo-Ortiz et al. 1999, most of the diagnostic characters of group *petersorum* are present. Exceptions are: the presence of dots on the flagellum; two additional distolateral tufts of setae on hypopharynx; stout setae on posterior apex of fore and middle legs; anal margin of the tergalii with both short and long setae. These characters remain unknown until complete re-examination of type material. Additionally, subapical setae are also not mentioned in the original description, but may have been overlooked. However, based on stacking videos, the fore legs of two paratypes have no subapical setae, other legs are not embedded in the slides (Lugo-Ortiz et al. 1999: 20).

MOTUs (see discussion in Kaltenbach et al. 2020). We studied specimens with the same morphology as *L. xeniolus*, collected in different locations far away from the type locality of *L. xeniolus* (Fig. 38a, b). The most important characters for the species assignment are: short, conical labial palp segment III; tergalii with remarkably strong development and pigmentation of tracheae; paraproct with poorly developed marginal spines. Based on COI sequences, we can distinguish seven different MOTUs (*L.* cf. *xeniolus* A–G; Table 1; Fig. 39). Unfortunately, a sequence from the type locality of *L. xeniolus* or nearby is lacking. We remain prudent and denominate these specimens as "cf. *xeniolus*". Interestingly, these specimens have all characters of the group *petersorum*, including subapical setae. This is pointing into the direction that *L. xeniolus* from the type locality equally might have all characters of the group *petersorum*, incl. subapical setae.

Material examined. *Labiobaetis xeniolus*. ***Paratypes.*** PAPUA NEW GUINEA • 2 larvae; Morobe Prov., Poverty Cr., Mt. Missim; 1600 m; 18.ix.1983; J.T. and D.A. Polhemus; on slides; PERC0012578, PERC0012579; Purdue University.

Labiobaetis cf. *xeniolus* A. PAPUA NEW GUINEA • larva; Western Highlands Prov., Simbai, Kairong River; 05°14'50"S, 144°28'27"E; 1850 m; 02.iii.2007; leg. Kinibel; (PNG 139); on slide; GBIFCH00829891; MZL • larva; Enga Prov., Wapanamanda; 05°38'06"S, 143°55'20"E; 1500 m; 06.xii.2006; leg. M. Balke and Kinibel; (PNG 128); on slide; GBIFCH00829892; MZL • larva; Madang Prov., Simbai area; 05°12'42"S, 144°35'31"E; 1800–2400 m; 08.iii.2007; leg. Kinibel; (PNG 151); on slide; GBIFCH00975618; MZL.

Labiobaetis cf. *xeniolus* B. PAPUA NEW GUINEA • 2 larvae; Central Prov., Tapini; 08°20'31"S, 146°59'49"E;

870 m; 29.x.2007; leg. Kinibel; (PNG 161); in alcohol; GBIFCH00515640, GBIFCH00829889; MZL • 1 larva; Central Prov., Kokoda Trek; 09°14'20"S, 147°40'32"E; 1400 m; i.2008; leg. Posman; (PNG 171); on slide; GBIFCH00829888; MZL.

Labiobaetis cf. *xeniolus* C. PAPUA NEW GUINEA • 16 larvae; Morobe Prov., Menyamya, Mt. Inji; nr 07°14'49"S, 146°01'20"E; 1700 m; 14.xi.2006; leg. M. Balke and Kinibel; (PNG 96); 1 on slide; GBIFCH00763703; 15 in alcohol; GBIFCH00829886; MZL.

Labiobaetis cf. *xeniolus* D. PAPUA NEW GUINEA • 2 larvae; Western Highlands Prov., Kundum; 05°16'06"S, 144°27'52"E; 1400 m; 03.iii.2007; leg. Kinibel; (PNG 142); 1 on slide; GBIFCH00975631; 1 in alcohol; GBIFCH00515635; MZL.

Labiobaetis cf. *xeniolus* E. PAPUA NEW GUINEA • 2 larvae; Central Prov., Kokoda Trek; 09°01'57"S, 147°44'27"E; 1400 m; i.2008; leg. Posman; (PNG 172); 1 on slide; GBIFCH00975627; 1 in alcohol; GBIFCH00515638; MZL.

Labiobaetis cf. *xeniolus* F. PAPUA NEW GUINEA • 6 larvae; Madang Prov., Simbai area; 05°13'23"S, 144°37'17"E; 1200 m; 10.iii.2007; leg. Kinibel; (PNG 152); 2 on slides; GBIFCH00515634, GBIFCH00763704; 4 in alcohol; GBIFCH00975619, GBIFCH00975668, GBIFCH00829896; MZL • 2 larvae; Madang Prov., Simbai area; 05°13'20"S, 144°37'37"E; 1200 m; 11.iii.2007; leg. Kinibel; (PNG 153); on slides; GBIFCH00515637, GBIFCH00975630; MZL.

Labiobaetis cf. *xeniolus* G. PAPUA NEW GUINEA • 4 larvae; Central Prov., Woitape; 08°31'35"S, 147°14'06"E; 1600 m; i.2008; leg. Posman; (PNG 165); 3 on slides; GBIFCH00592681, GBIFCH00975666, GBIFCH00829894; 1 in alcohol; GBIFCH00515627; MZL.

3. *Labiobaetis gladius* Kaltenbach & Gattolliat, 2018

Labiobaetis gladius: Kaltenbach and Gattolliat 2018.

Additional description. Larva. Re-examination of type material confirmed that the species has all of the diagnostic characters of the group *petersorum* as listed above. This includes characters not or not correctly described or illustrated in the original description (Kaltenbach and Gattolliat 2018: figs 17–18): flagellum with brown dots in middle part (as Fig. 6b); hypopharynx distolaterally with two additional tufts of setae (as Fig. 3a); anal margin of tergalii with both short and long, fine setae (as Fig. 6e); claw with convex ventral margin and with subapical seta (as Fig. 5k, l); femur posterior apex with stout setae on fore and middle legs, not on hind leg (as Fig. 5e).

Material examined. ***Paratypes.*** PAPUA NEW GUINEA • 3 larvae; Simbu Prov., Mt. Wilhelm, Pindaunde Creek, S5 (oria 6); 05°49'58"S, 145°06'08"E; 2350 m; 18.viii.1999; leg. L. Čížek; on slides; GBIFCH00456173, GBIFCH00465177, GBIFCH00456178; MZL.

4. *Labiobaetis janae* Kaltenbach & Gattolliat, 2018

Labiobaetis janae: Kaltenbach and Gattolliat 2018.

Additional description. Larva. Re-examination of type material confirmed that the species has most of the diagnostic characters of the group *petersorum* as listed above. This includes characters not or not correctly described or illustrated in the original description (Kaltenbach and Gattolliat 2018: figs 19–20): hypopharynx distolaterally with two additional tufts of setae (as Fig. 3a); anal margin of tergalii with both short and long, fine setae (as Fig. 6e); claw with very slightly convex ventral margin; claw with subapical seta (as Fig. 5l); femur posterior apex with stout setae on fore and middle legs, not on hind leg (as Fig. 5e). The flagellum has no brown dots, as it is usually the case in the group *petersorum*.

Material examined. ***Paratypes.*** INDONESIA • Papua Prov., Lake Habemma, stream; 04°07'46"S, 138°40'46"E; 3200 m; 19.x.2011; leg. M. Balke; (PAP07); on slide; GBIFCH00465182; MZL.

5. *Labiobaetis amber* sp. nov.

https://zoobank.org/289249EE-9562-44D6-A5F5-A602900CB96A

Figs 1–7, 38

Diagnosis. Larva. Following combination of characters differentiates *L. amber* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 2a); B) both mandibles without denticles between prostheca and mola (Fig. 2d, f); C) labial palp segment II with broadly rounded, thumb-like, distomedial protuberance; segment III nearly oblong (Fig. 4d); D) paraglossa dorsally with row of four long, spine-like setae near inner, distal margin (Fig. 4c); E) tibia with row of medium, stout, apically rounded setae on dorsal margin (Fig. 5f); posterior surface scattered with short, lanceolate setae (Fig. 5h); F) claw with ca. ten denticles (Fig. 5k); G) posterior margin of abdominal tergum IV with triangular, pointed spines, mostly slightly wider than long (Fig. 6c).

Description. Larva (Figs 1–7). Body length 6.2–8.2 mm. Cerci: ca. 3/4 of body length. Paracercus: ca. 1/2 of cerci length. Antenna: approx. twice as long as head length.

Cuticular colouration (Fig. 1a, b). Head, thorax and abdomen dorsally mainly brown, with pattern as in Fig. 1a. Forewing pads light brown with dark brown and grey stripes; abdominal tergum I grey with brown streak along distal margin; terga II–IV grey-brown, laterally brighter, with distolateral brown spots; terga V–VI off-white, laterally with darker areas; terga VII–VIII dark brown, laterally with whitish streak, medially with light brown line; tergum IX grey-brown with bright area medially; tergum X off-white. Thorax and abdomen ventrally grey-white, sterna VII–VIII darker. Legs off-white, femur medially with large grey area, with large blanks in distal and proximal area; tarsus distally grey-brown. Caudalii grey.

Figure 1. *Labiobaetis amber* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars: 1 mm.

Hypodermal colouration (Fig. 6b). Antenna with dark brown dots in middle part of flagellum.

Antenna (Fig. 6a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 2a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. ten long, simple setae. Ventrally with marginal row of setae composed of lateral and anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 2c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with four denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, smooth. Tuft of setae at apex of mola present.

Left mandible (Fig. 2e, f). Incisor and kinetodontium fused. Incisor with four denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, smooth. Subtriangular process rather short, basally broad, above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 3a). Lingua approx. as long as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins angulate; fine, long, simple setae along distal margin.

Maxilla (Fig. 3b, d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered, spine-like seta and ca. six long, simple setae. Maxillary palp slightly longer than length of galea-lacinia; 2-segmented; palp segment II slightly longer and narrower than segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 4a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. nine spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. five spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and ca. two short, simple setae in anteromedial area; dorsally with four long, spine-

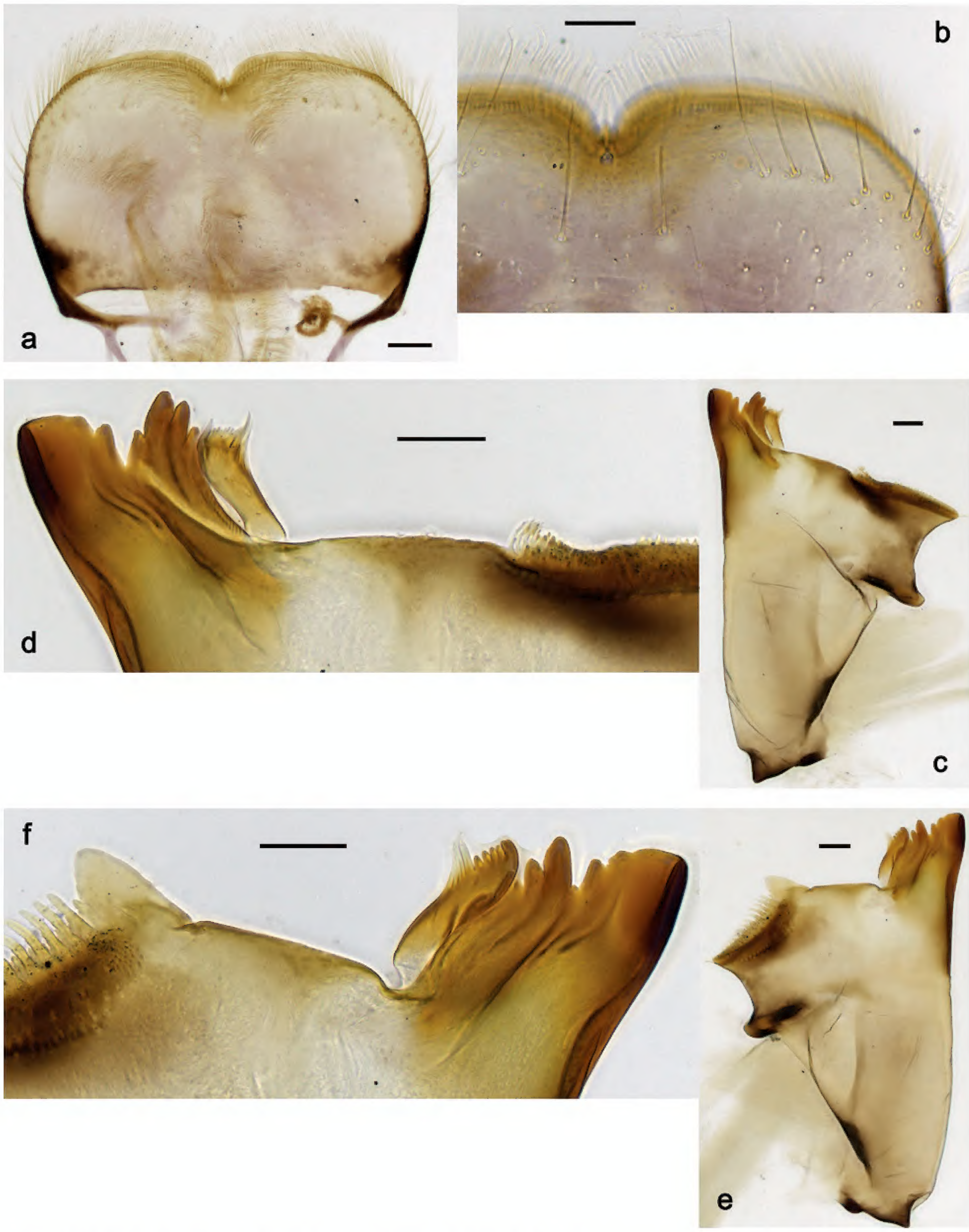

Figure 2. *Labiobaetis amber* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e, f.** Left mandible. Scale bars: 50 µm.

like setae near inner margin. Labial palp with segment I slightly shorter than length of segments II and III combined. Segment II with broadly rounded, thumb-like, distomedial protuberance; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. six spine-like setae near outer margin. Segment III nearly oblong; length 1.1× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

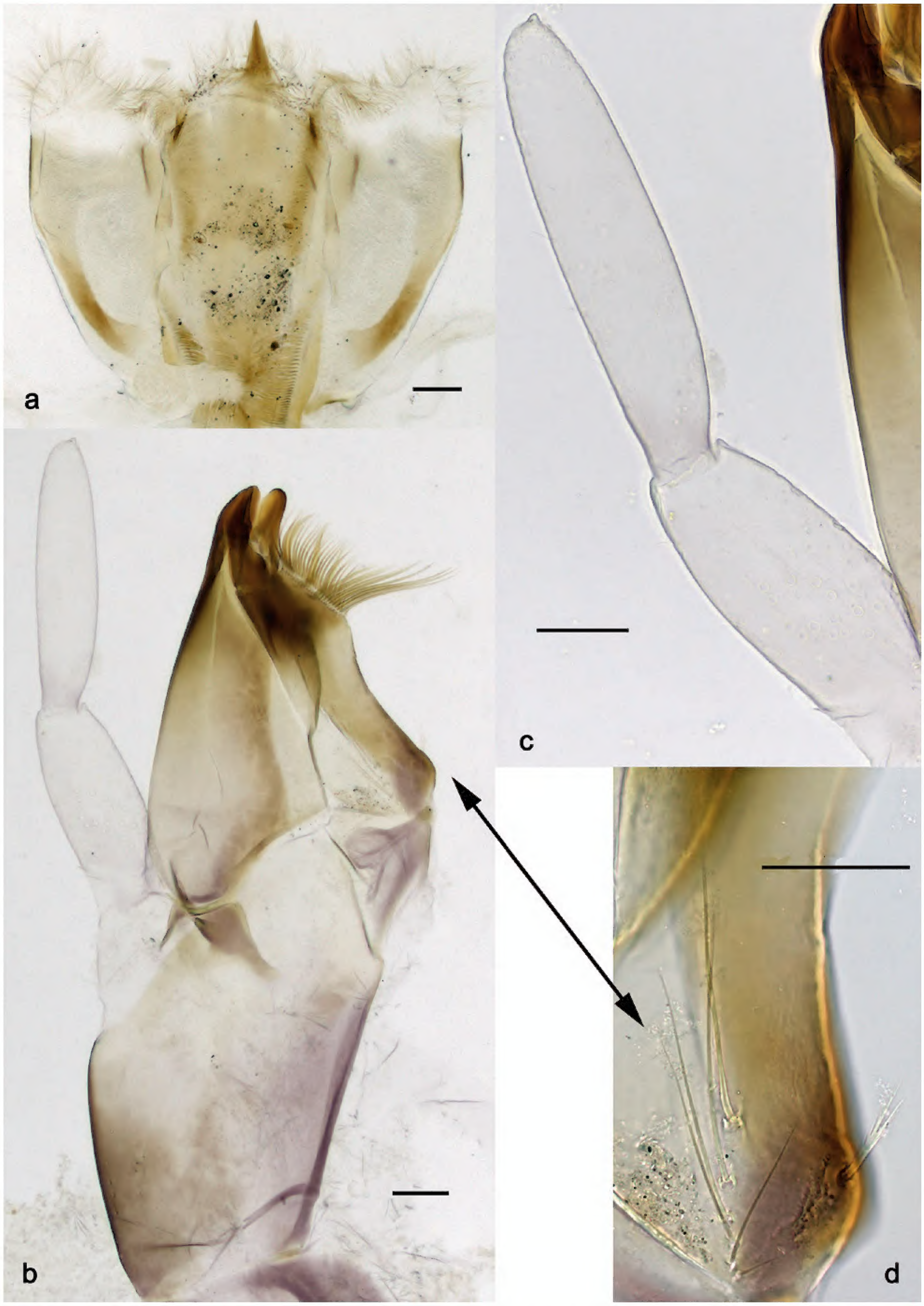

Figure 3. *Labiobaetis amber* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

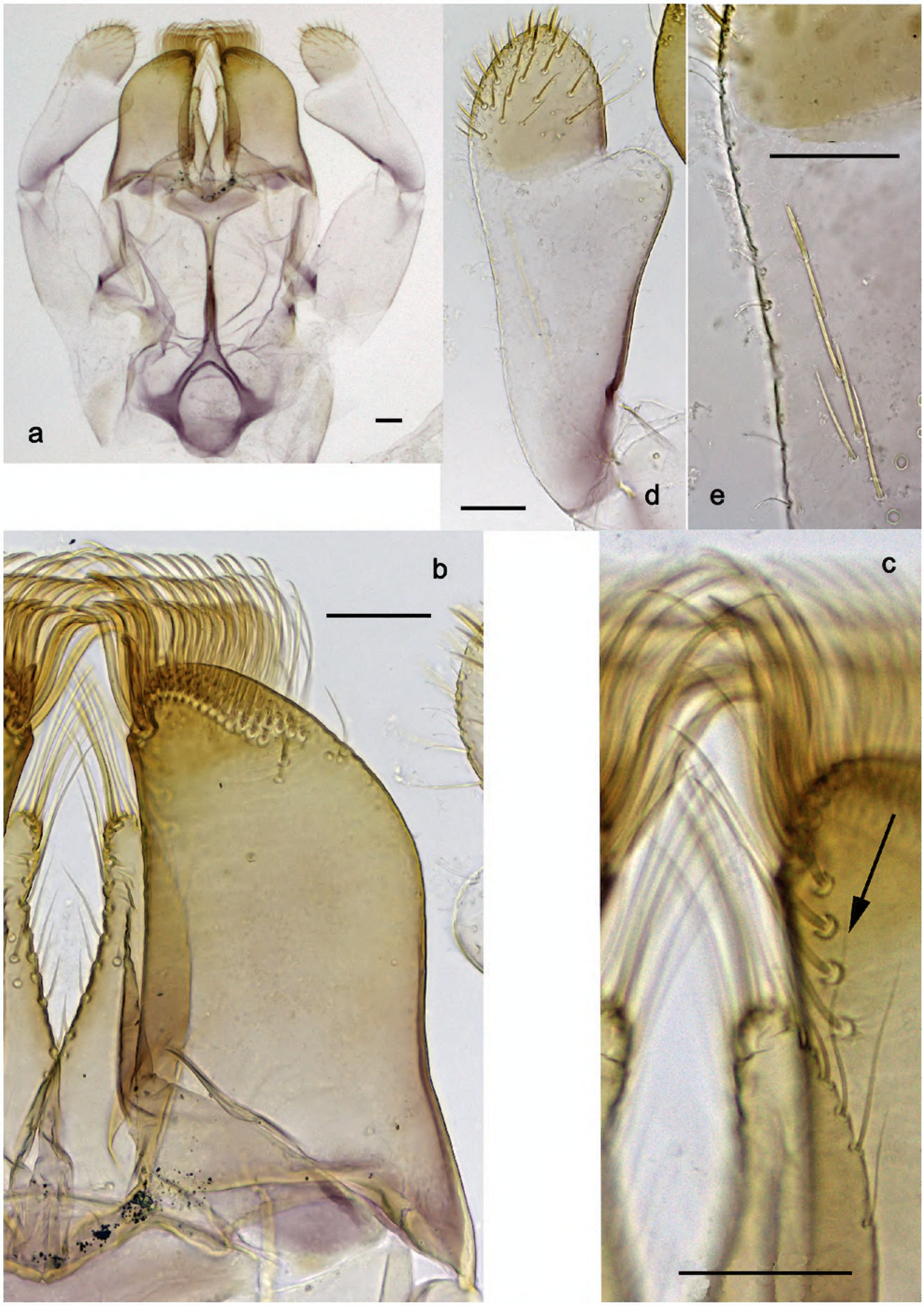

Figure 4. *Labiobaetis amber* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 μm.

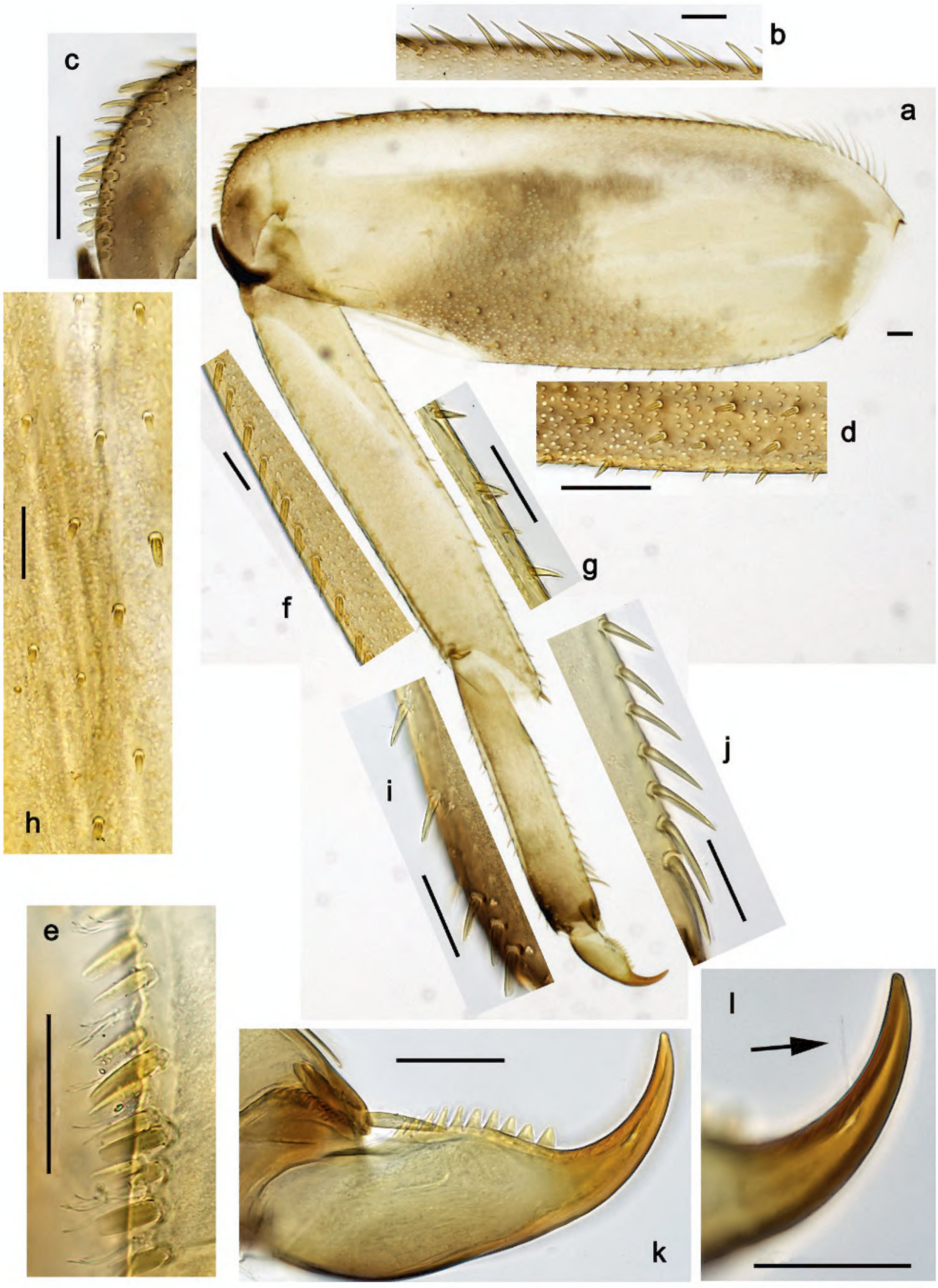

Figure 5. *Labiobaetis amber* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, apex; **d.** Fore femur, ventral margin; **e.** Fore femur, apex, posterior side; **f.** Fore tibia, dorsal margin; **g.** Fore tibia, ventral margin; **h.** Fore tibia, posterior surface; **i.** Fore tarsus, dorsal margin; **j.** Fore tarsus, ventral margin; **k.** Fore claw; **l.** Tip of fore claw. Scale bars: 50 µm.

Figure 6. *Labiobaetis amber* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct; **g.** Larval protogonostylus (II, III: segments II and III). Scale bars: 50 µm.

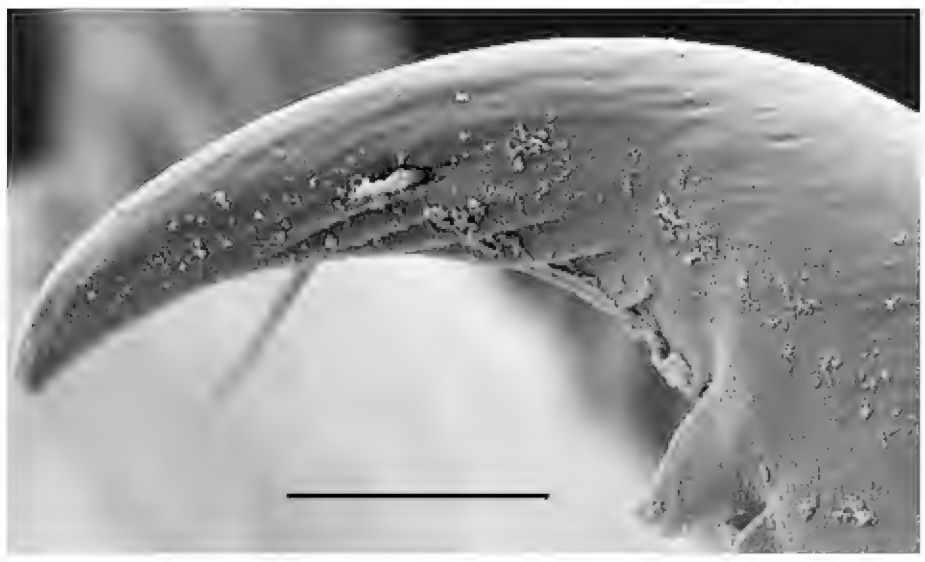

Figure 7. *Labiobaetis amber* sp. nov., larva, distal part of fore claw with subapical setae; SEM picture. Scale bar: 20 µm.

Legs (Figs 5a–k, 7). Ratio of foreleg segments 1.4:1.0:0.6:0.2. ***Femur.*** Fore femur length ca. 2.7× maximum width, middle and hind femur less wide. Dorsal margin with a row of ca. 50 curved, spine-like setae; length of setae 0.16× maximum width of femur. Apex rounded, with many short, stout, lanceolate setae. Apex on posterior side with short, stout, apically truncate setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin, few such setae on surface of distomedial half; femoral patch reduced on fore and middle leg, well developed on hind leg. ***Tibia.*** Dorsal margin with row of medium, stout, apically rounded setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate setae along patellatibial suture. Posterior surface with short, stout, apically rounded, scattered setae. Patellatibial suture present on basal half. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. ten denticles; distally pointed; with long, fine, transparent subapical seta on posterior side and short subapical seta on anterior side.

Abdominal terga (Fig. 6c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–VII with triangular spines, mostly slightly wider than long; VIII–IX with spines becoming slenderer and longer.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 6d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and ½ VI combined. Tergalius VII as long as length of segment VIII and ½ IX combined.

Paraproct (Fig. 6f). Distally not expanded, with ca. 33 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. With reference to Amber village, the type locality of the species.

Distribution. Indonesia, Papua Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 1200 m.

Type material. ***Holotype.*** INDONESIA • larva; Papua Prov., River Je, Loc. Arfak, East of Amber village; 01°10'59"S, 133°54'44"E; 1200 m; 16.vi.2016, leg. Sumoked and M. Balke; (BH 68); on slide; GBIFCH00763716; MZB. ***Paratypes.*** INDONESIA • 28 larvae; same data as holotype; 2 on slides; GBIFCH00763717, GBIFCH00592774; MZL; 23 in alcohol; GBIFCH00515646, GBIFCH00515647, GBIFCH00975600, GBIFCH00975607, GBIFCH00975712; MZL.

6. *Labiobaetis bilibil* sp. nov.

https://zoobank.org/0AC9992D-3D71-47B1-824D-81526F0B9C5D

Figs 8–13, 38

Diagnosis. Larva. Following combination of characters differentiates *L. bilibil* sp. nov. from other species of the group *petersorum*: A) labrum length 0.5× maximal width (Fig. 9a); B) both mandibles with row of minute denticles between prostheca and mola (Fig. 9e, h); C) labial palp segment II with extended, slightly hooked, distomedial protuberance; segment III conical (Fig. 10c); D) paraglossa dorsally with row of 2–4 long, spine-like setae near inner, distal margin (Fig. 10b); E) tibia with row of short and medium, stout, lanceolate, pointed setae on dorsal margin (Fig. 12a, e); posterior surface scattered with short, lanceolate setae (Fig. 12g); F) claw with ca. eight denticles (Fig. 12k); G) posterior margin of abdominal tergum IV with triangular, pointed spines, longer than wide (Fig. 13c).

Description. Larva (Figs 8–13). Body length 8.8–9.5 mm. Cerci: broken. Paracercus: ca. 0.4× body length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 8a, b). Head, thorax and abdomen dorsally brown, with pattern as in Fig. 8a. Forewing pads light brown with dark brown and grey stripes; abdominal terga II–IV and VII–VIII darker. Thorax ventrally grey; abdominal sternum I grey, II–V beige and VI–X light brown to brown. Legs brown with brighter areas, femur with elongate proxomedial and distodorsal blanks. Caudalii light brown.

Hypodermal colouration (Fig. 13b). Antenna with dark brown dots in middle part of flagellum.

Antenna (Fig. 13a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 9a, b). Sub-rectangular, length 0.5× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. ten long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 9c–e). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles,

Figure 8. *Labiobaetis bilibil* sp. nov., larva habitus:; **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 9f–h). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 10a). Lingua longer as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally slightly expanded. Superlinguae distolaterally protruding; lateral margins angulate; fine, long, simple setae along distal margin.

Maxilla (Fig. 10b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. as long and much narrower as segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically slightly pointed, constricted.

Labium (Fig. 11a–d). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. seven spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and one short, simple seta in anteromedial area; dorsally with 2–4 long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with elongate, slightly hooked distomedial protuberance; distomedial protuberance 0.6× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III conical; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 12a–k). Ratio of foreleg segments 1.6:1.0:0.7:0.2. ***Femur.*** Fore femur length ca. 2.3× maximum width, middle and hind femur less wide. Dorsal margin with a row of ca. 55 curved, spine-like setae, in proximal part a partial 2nd row; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, spine-like, pointed setae. Apex on posterior side with short, stout, apically pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin, few such setae on surface of distomedial half; femoral patch reduced on fore and middle leg, well developed on hind leg. ***Tibia.*** Dorsal margin with row of short and medium, stout, lanceolate, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae.

Anterior surface with short, stout, lanceolate, pointed setae mostly along patellatibial suture. Posterior surface with short, stout, apically rounded, scattered setae. Patellatibial suture present on basal 4/5 area. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally, and row of short, spine-like setae near ventral margin. Claw with one row of ca. eight denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

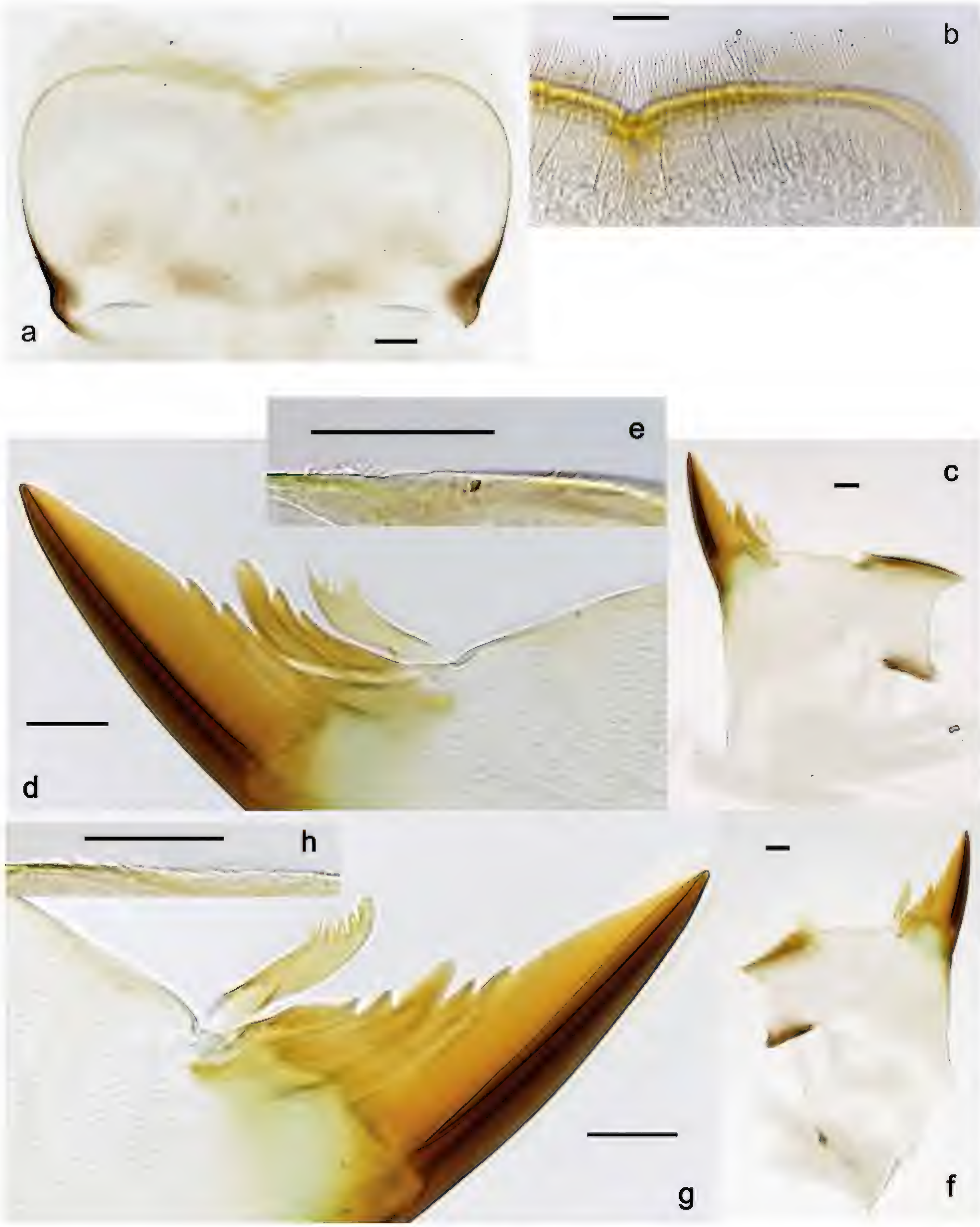

Figure 9. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola. Scale bars: 50 µm.

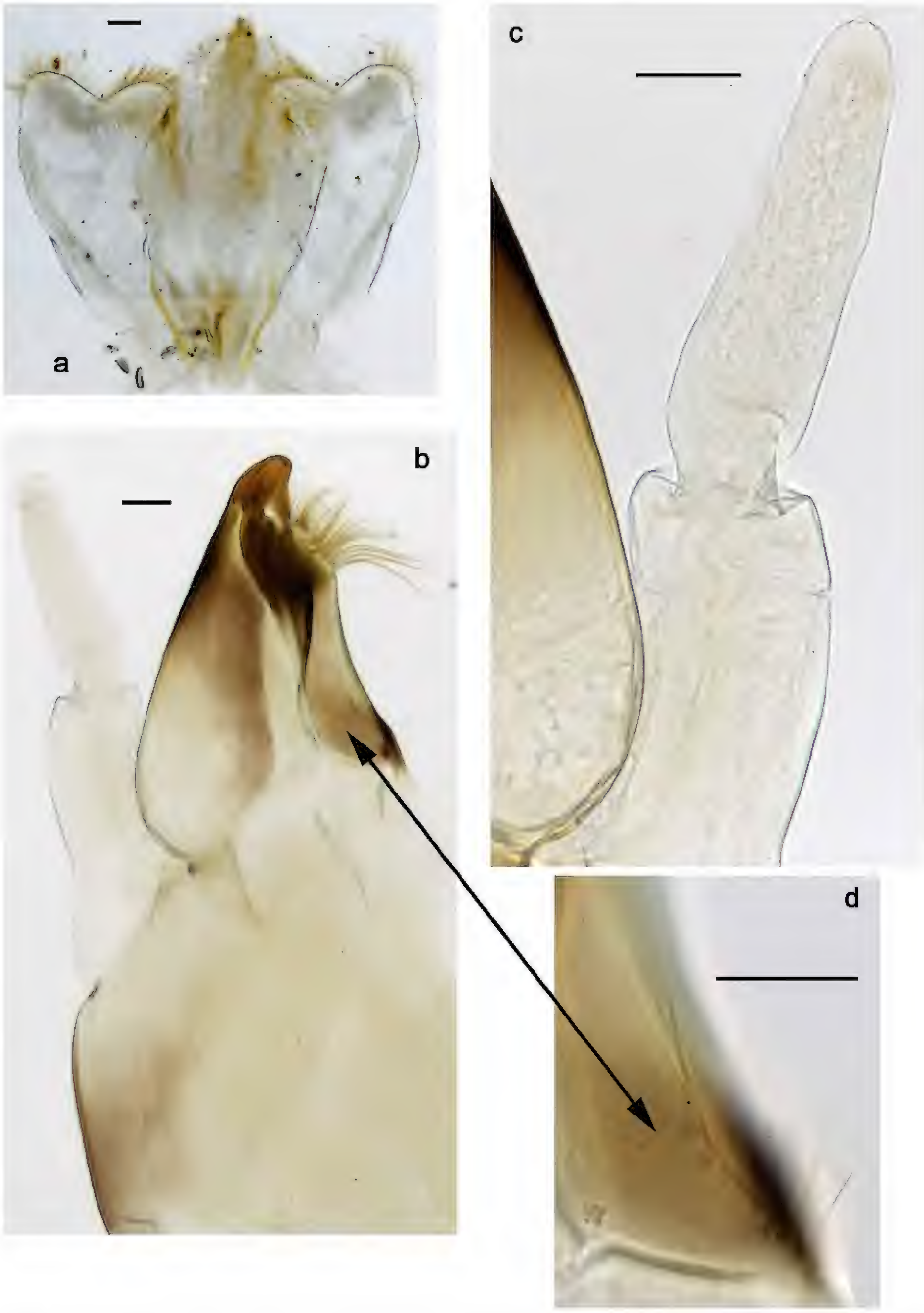

Figure 10. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

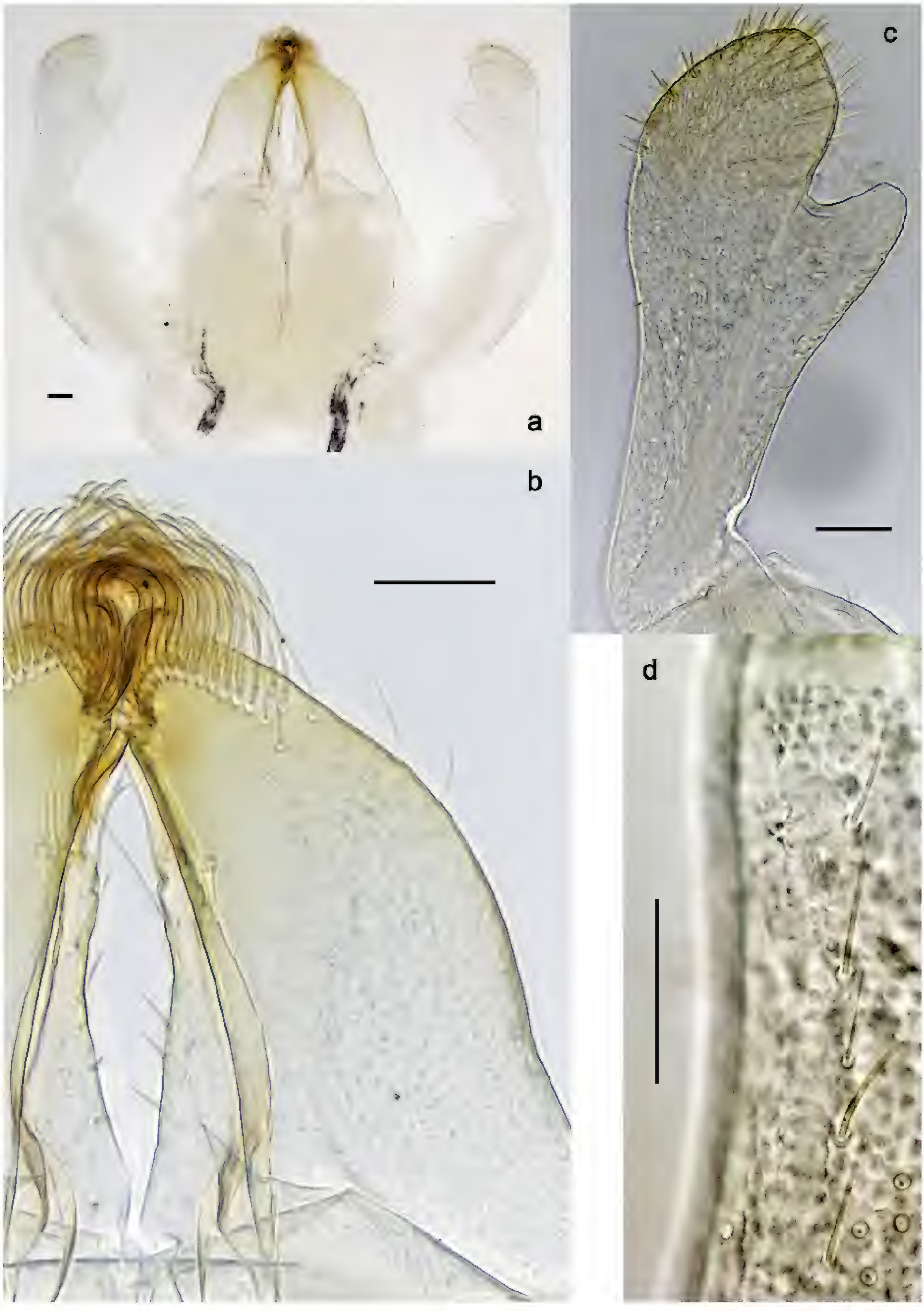

Figure 11. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Labial palp, ventral focus; **d.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Figure 12. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tibia, posterior surface; **h.** Fore tarsus, dorsal margin; **i.** Fore tarsus, ventral margin; **j.** Tip of fore claw; **k.** Fore claw. Scale bars: 50 µm.

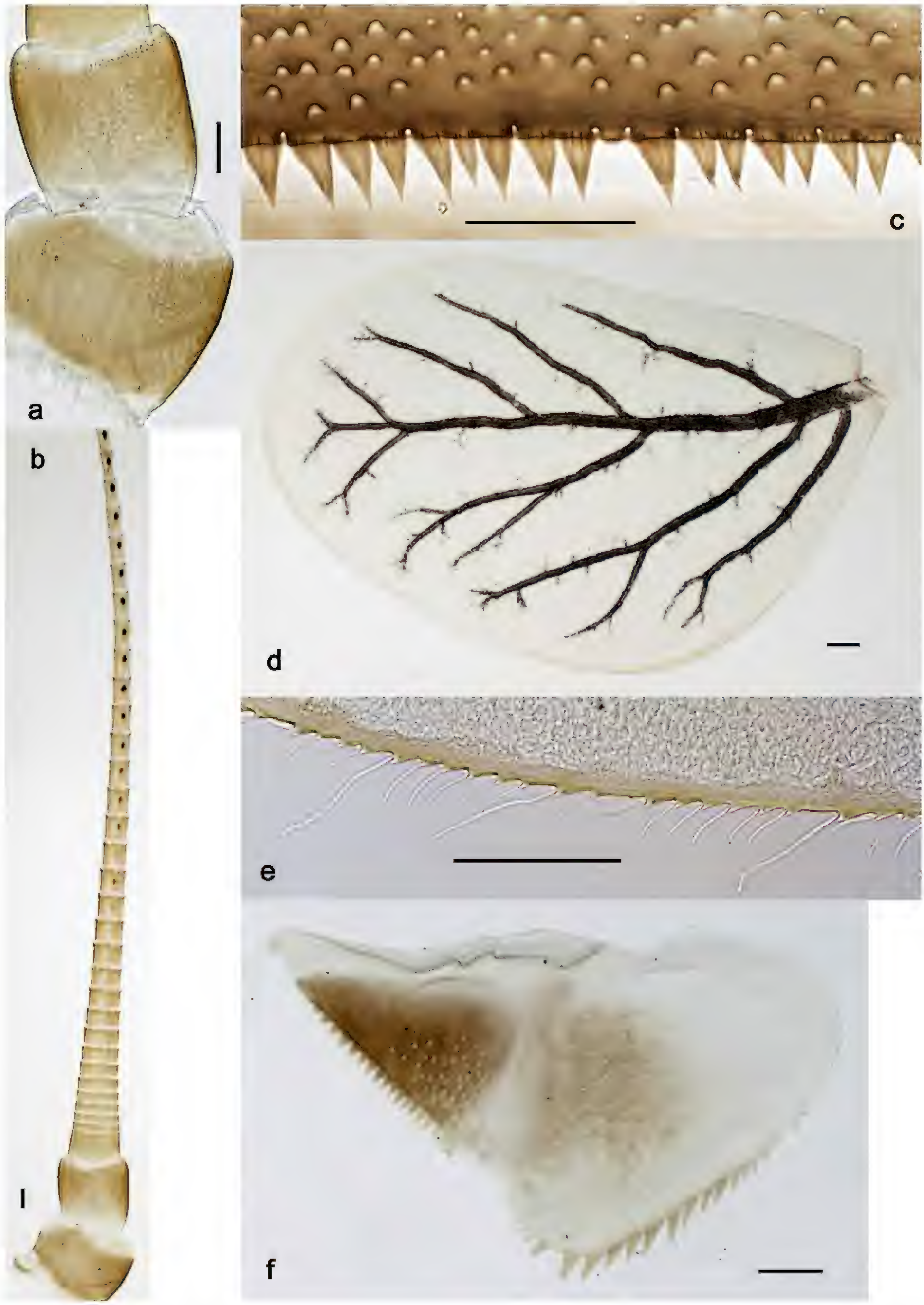

Figure 13. *Labiobaetis bilibil* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

Abdominal terga (Fig. 13c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–IX with triangular, sharply pointed spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–V smooth, without spines; VI–IX with small, triangular spines.

Tergalii (Fig. 13d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and VI combined. Tergalius VII as long as length of segments VIII and ½ IX combined.

Paraproct (Fig. 6f). Distally not expanded, with ca. 21 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the indigenous Bilibil people of the Madang region, where the type locality is.

Distribution. Papua New Guinea (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 350 m.

Type material. ***Holotype.*** PAPUA NEW GUINEA • larva; Madang Prov., Adalbert Mts., Sewan; 04°41'01"S, 145°26'55"E, 350 m; 03.v.2006; leg. M. Balke and Manaono; (PNG 50); on slide; GBIFCH00592772; ZSM. ***Paratypes.*** PAPUA NEW GUINEA • 19 larvae; same data as holotype; 4 on slides; GBIFCH00592571, GBIFCH00592572, GBIFCH00592573, GBIFCH00763602; MZL; 15 in alcohol; GBIFCH00515641, GBIFCH00515642, GBIFCH00975601, GBIFCH00975616, GBIFCH00975711; MZL.

7. *Labiobaetis kinibeli* sp. nov.

https://zoobank.org/4E9B39F3-B746-46E9-8F06-8439008961F6

Figs 14–19, 38

Diagnosis. Larva. Following combination of characters differentiates *L. kinibeli* sp. nov. from other species of the group *petersorum*: A) labrum length 0.55× maximal width (Fig. 15a); B) both mandibles with row of minute denticles between prostheca and mola; subtriangular process of left mandible with minute denticles on basal outer margin (Fig. 15e, h, i); C) labial palp segment II with thumb-like, apically rounded distomedial protuberance; segment III slightly pentagonal (Fig. 17d); D) paraglossa dorsally with row of four long, spine-like setae near inner, distal margin (Fig. 17c); E) fore tibia with two rows of short, stout, lanceolate, pointed setae on dorsal margin (Fig. 18a, e); posterior surface without scattered, stout setae; F) claw with ca. eight denticles (Fig. 12k); G) posterior margin of abdominal tergum IV with triangular spines, mostly slightly wider than long (Fig. 19c).

Figure 14. *Labiobaetis kinibeli* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

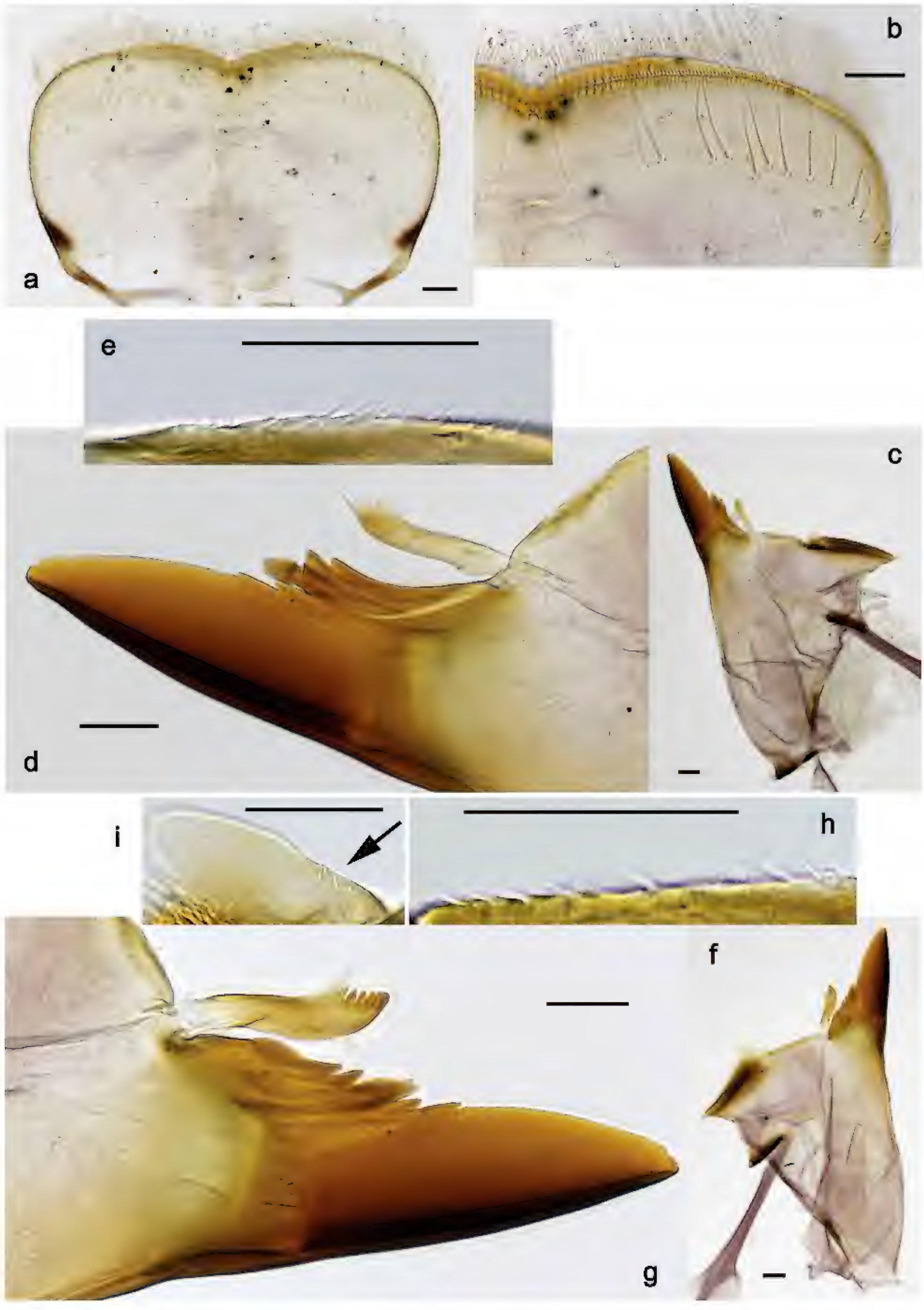

Figure 15. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola; **i.** Left mandible, subtriangular process. Scale bars: 50 µm.

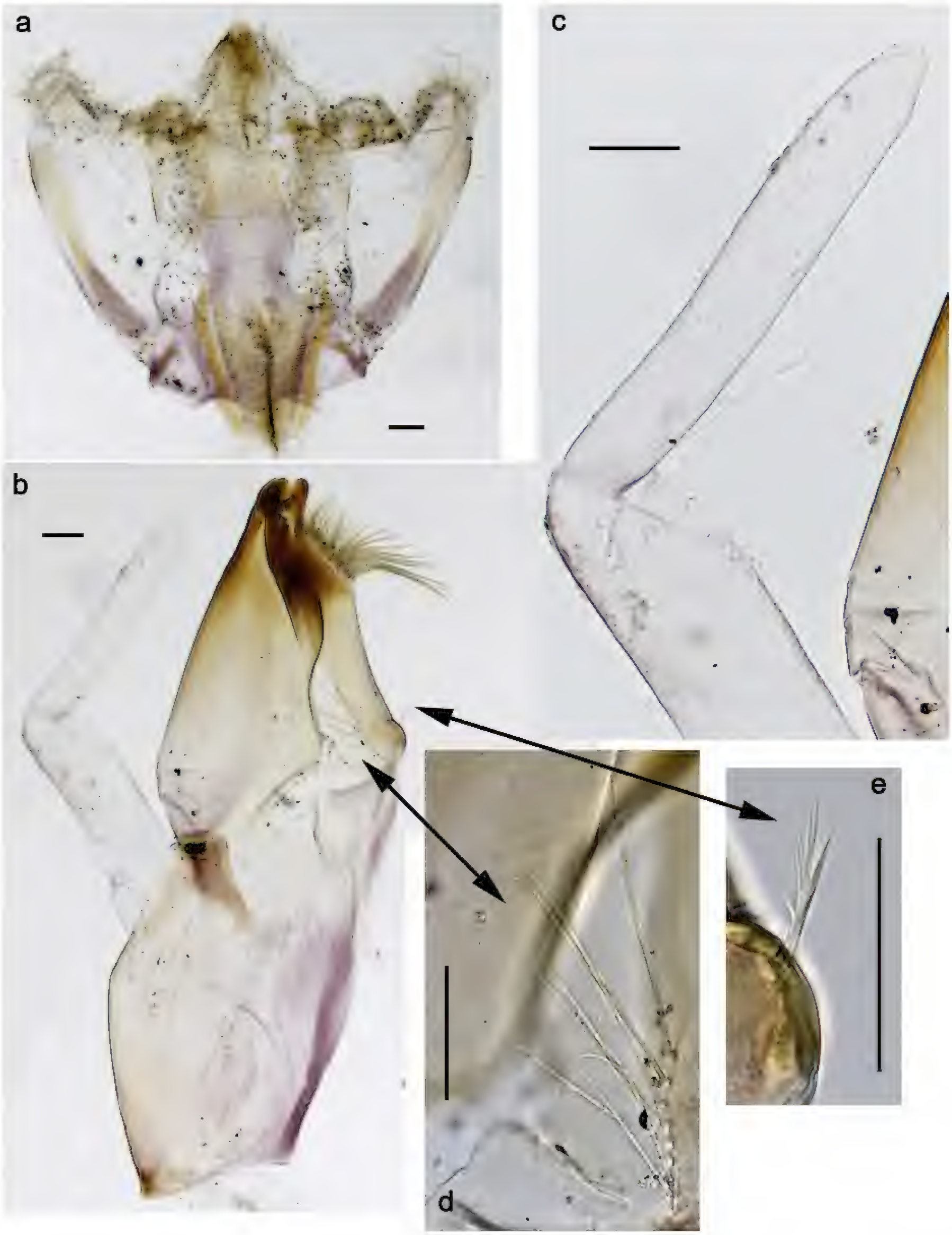

Figure 16. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d, e.** Sections of maxilla. Scale bars: 50 μm.

Description. Larva (Figs 14–19). Body length 7.6–8.5 mm. Cerci: ca. 2/3 of body length. Paracercus: ca. 0.8× cerci length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 14a, b). Head, thorax and abdomen dorsally reddish-brown. Abdominal terga IX–X brighter. Thorax ventrally off-white; abdominal sterna light reddish-brown. Legs brown with, femur with elongate proxomedial and distodorsal blanks. Caudalii light brown.

Hypodermal colouration. Antenna with dark brown dots in middle part of flagellum (Fig. 19b). Abdominal intersegmental membranes with dark purple-brown anterior margins (Fig. 14a).

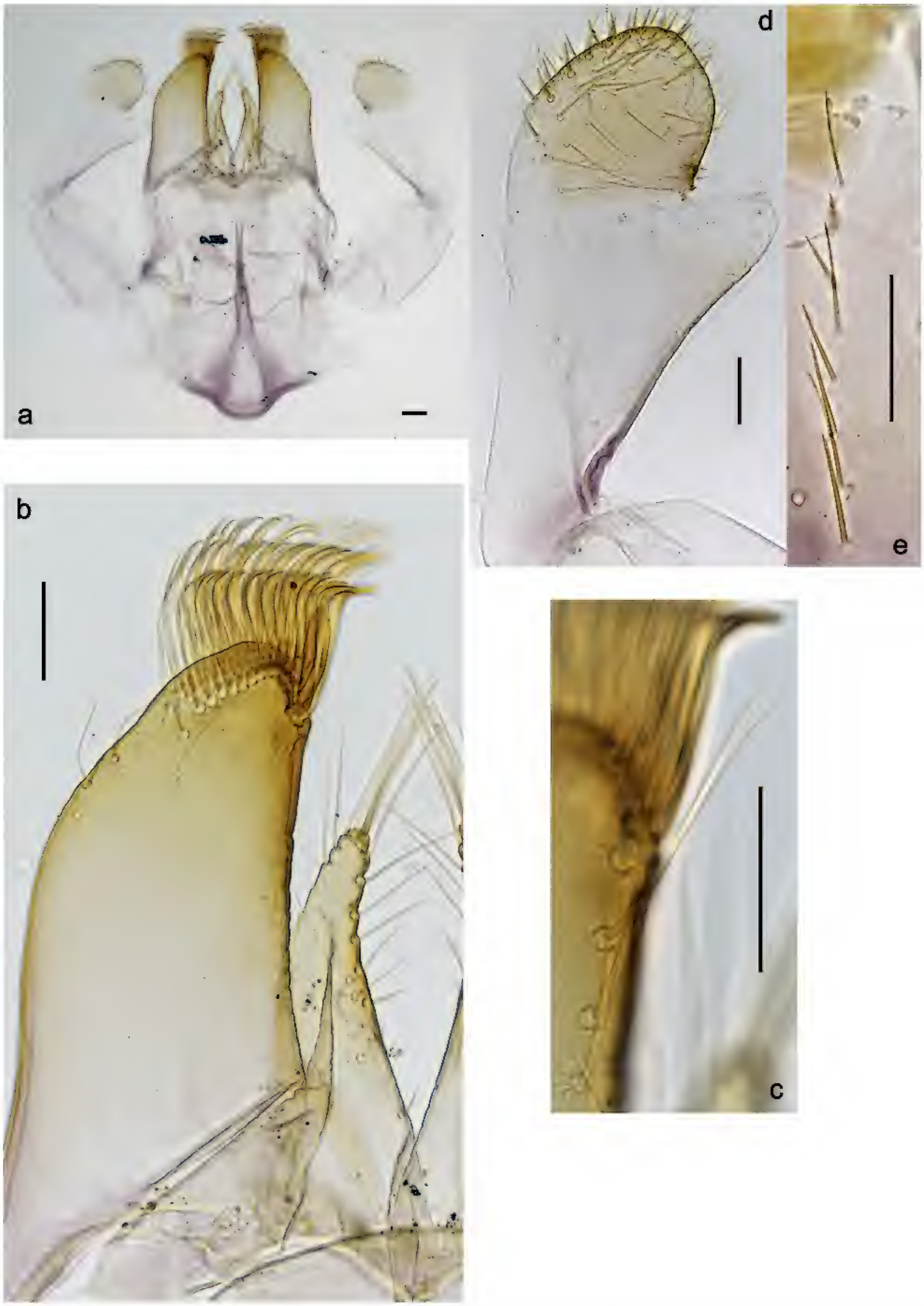

Figure 17. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Figure 18. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tarsus, dorsal margin; **g.** Fore claw. Scale bars: 50 µm.

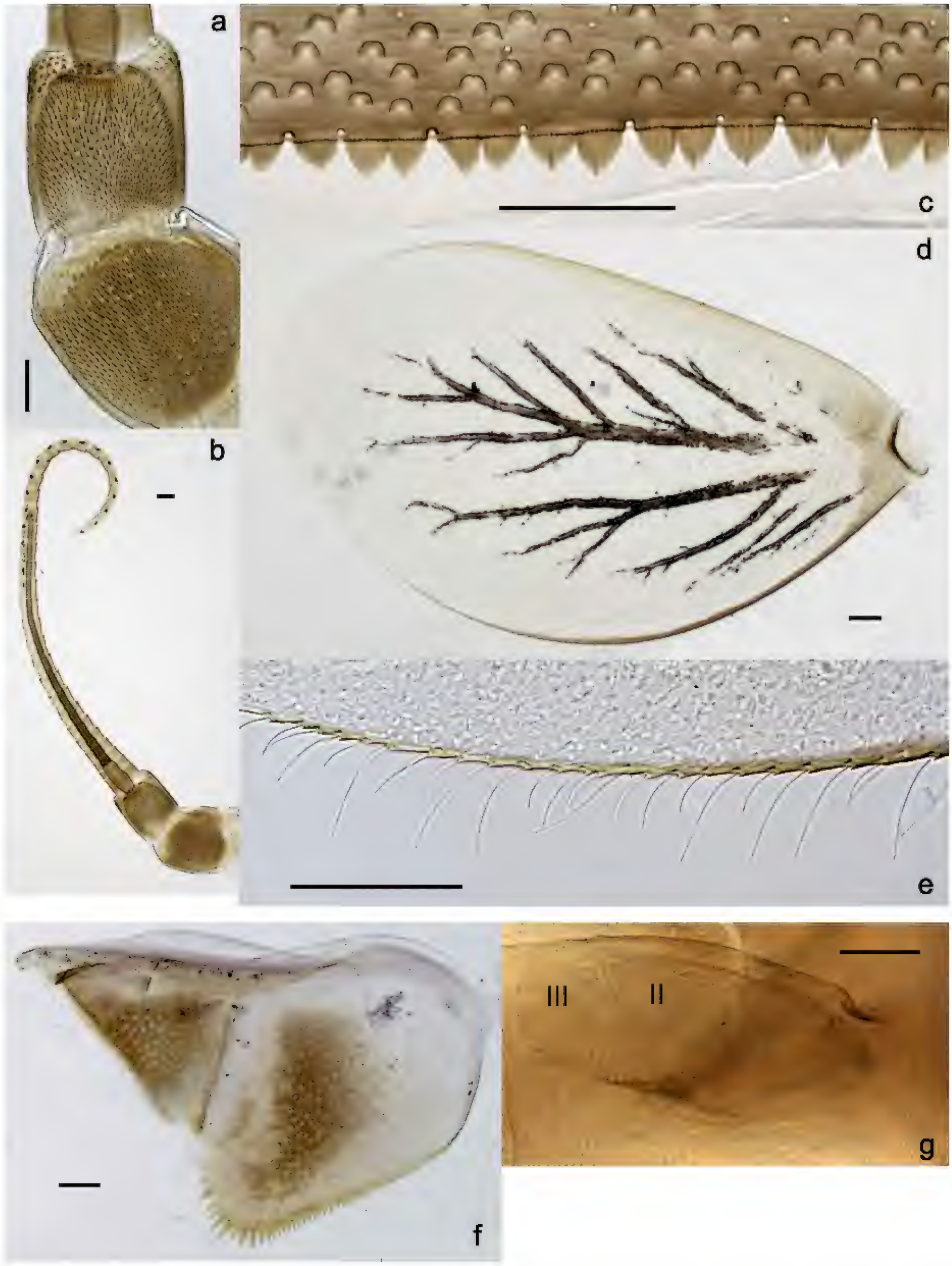

Figure 19. *Labiobaetis kinibeli* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct; **g.** Larval protogonostylus (II, III: segments II and III). Scale bars: 50 µm.

Antenna (Fig. 19a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 15a, b). Sub-rectangular, length 0.55× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. 13 long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 15c–e). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles,

inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 15f–i). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola, basally on outer margin with minute denticles Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 16a). Lingua longer as superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 16b–e). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. 1.2× as long as segment I, and much narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 17a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. nine spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and one short, simple seta in anteromedial area; dorsally with row of four long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, apically rounded, distomedial protuberance; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. eight spine-like setae near outer margin. Segment III slightly pentagonal; length approx. 0.9× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 18a–g). Ratio of foreleg segments 1.4:1.0:0.5:0.2. ***Femur.*** Fore femur length ca. 2.5× maximum width, middle and hind femur less wide. Dorsal margin with row of ca. 43 curved, spine-like setae; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, spine-like, pointed setae. Apex on posterior side with short, stout, apically pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch absent on fore leg, rudimentary on middle leg, and reduced on hind leg. ***Tibia.*** Dorsal margin of fore leg with two rows of short, stout, lanceolate, pointed setae, 2nd row poorly developed on middle leg and only one row on hind leg. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae in distal part and along patellatibial suture. Posterior surface without stout setae in dorsal half, some stout setae in ventral half along patellatibial suture. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with row of short, spine-like setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. eight denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 19c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II with rudimentary, rounded spines; III–VI with triangular spines, mostly slightly wider than long; VII–IX with triangular spines, longer than wide; mostly 2–3 spines basally fused.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 19d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V and VI combined. Tergalius VII as long as length of segments VIII and 3/4 IX combined.

Paraproct (Fig. 19f). Distally not expanded, with ca. 53 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the successful collector of the specimens, Mr. Kinibel (Papua New Guinea).

Distribution. Papua New Guinea (Fig. 38a).

Biological aspects. The specimens were collected at altitudes between 900 m–2000 m, partly together with *Labiobaetis gindroi* Kaltenbach & Gattolliat, 2018 and *Labiobaetis rutschmannae* Kaltenbach & Gattolliat, 2018.

Type material. ***Holotype.*** PAPUA NEW GUINEA • larva; Western Highlands Prov., Lugup River; 05°17'14"S, 144°28'13"E; 1700 m; 04.iii.2007; leg. Kinibel; (PNG 143); on slide; GBIFCH00975628; ZSM. ***Paratypes.*** PAPUA NEW GUINEA • 6 larvae; same data as holotype; 1 on slide; GBIFCH00975609; MZL; 5 in alcohol; GBIFCH00515639, GBIFCH00975665, GBIFCH00975667; MZL • 1 larva; Central Prov., Tapini, Loloipa River; near 08°20'31"S, 146°59'49"E; 940 m; 31.x.2007; leg. Kinibel; (PNG 163); on slide; GBIFCH00829887; MZL • 3 larvae; Western Highlands Prov., Simbai; 05°15'10"S, 144°32'49"E; 2000 m; 28.ii.2007; leg. Kinibel; (PNG 136); 1 on slide; GBIFCH00975632; MZL; 2 in alcohol; GBIFCH00515633; MZL • 2 larvae; Western Highlands, Simbai; 05°15'52"S, 144°32'43"E; 1800–2000 m; 26.ii.2007; leg. Kinibel; (PNG 134); 1 in alcohol; GBIFCH00975760; 1 on slide; GBIFCH00763775; MZL.

8. *Labiobaetis nabire* sp. nov.

https://zoobank.org/9CCF94C8-B0BD-499D-93DA-BA6CC143420A

Figs 20–25, 38

Diagnosis. Larva. Following combination of characters differentiates *L. nabire* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 21a); B) both mandibles with smooth margin between prostheca and mola (Fig. 21c, e); C) labial palp segment II with thumb-like, distomedial protuberance, distal margin of protuberance slightly concave; segment III oblong (Fig. 23d); D) paraglossa dorsally with two long, spine-like setae near inner, distal margin (Fig. 23c); E) tibia with row of short, stout, apically rounded setae on dorsal margin (Fig. 24e); posterior surface without scattered, stout setae; F) claw with ca. nine denticles (Fig. 24g); G) posterior margin of abdominal tergum IV with triangular spines, mostly slightly wider than long (Fig. 25c); H) legs with hypodermal, oblong, orange-brown spot medially on posterior side of femur (Fig. 20a).

Description. Larva (Figs 20–25). Body length 6.3–7.2 mm. Cerci: nearly as long as body length. Paracercus: ca. 0.5× cerci length. Antenna: approx. 2.5× as long as head length.

Cuticular colouration (Fig. 20a, b). Head, thorax and abdomen dorsally grey-brown, with pattern as in Fig. 20a. Abdominal terga VI, IX and partly X brighter; I–IX laterally with bright marks. Thorax and abdomen ventrally off-white. Legs with different shades of grey and brown as in Fig. 20b; femur with elongate proxomedial and distodorsal blanks. Caudalii grey-brown.

Hypodermal colouration. Antenna with dark brown dots in middle part of flagellum (Fig. 25b). Abdominal intersegmental membranes in distal part of abdomen with dark brown anterior margins (Fig. 20a). Femora on posterior side with medial, oblong, orange-brown spots (Fig. 20a).

Figure 20. *Labiobaetis nabire* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

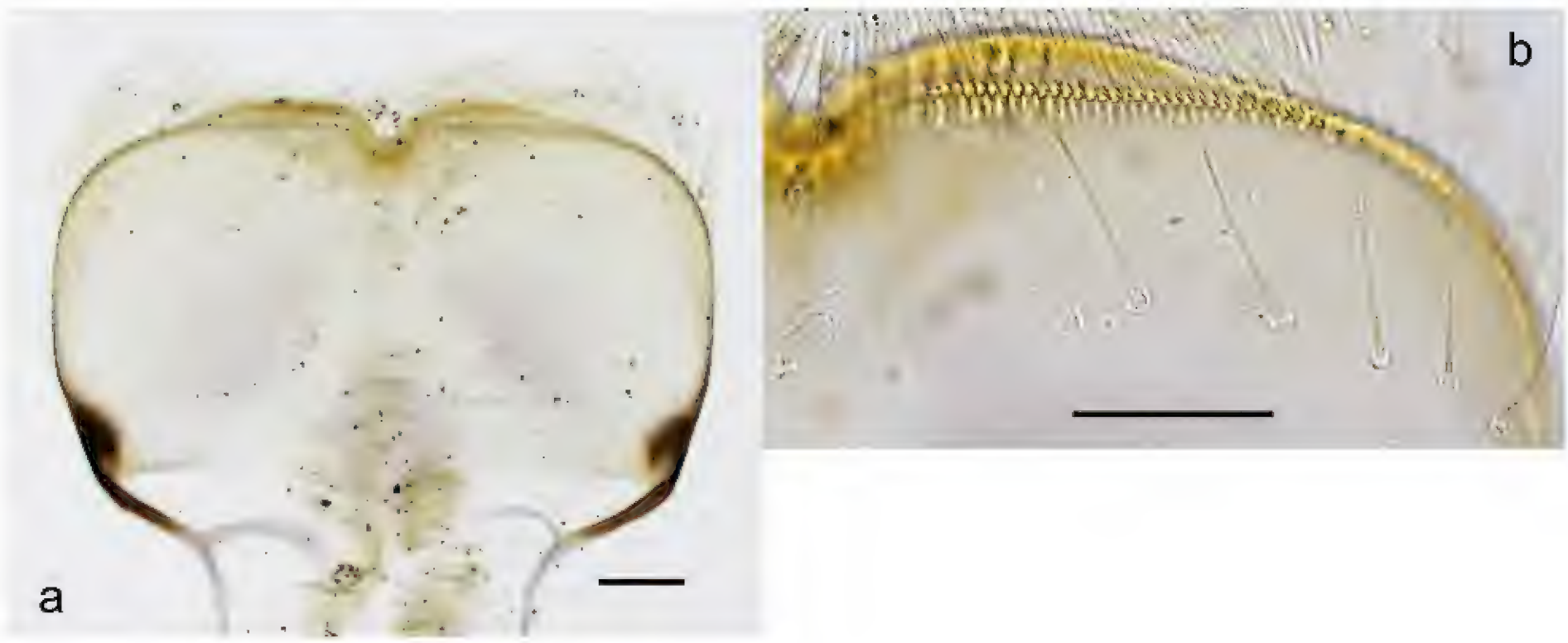

Figure 21. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e, f.** Left mandible. Scale bars: 50 µm.

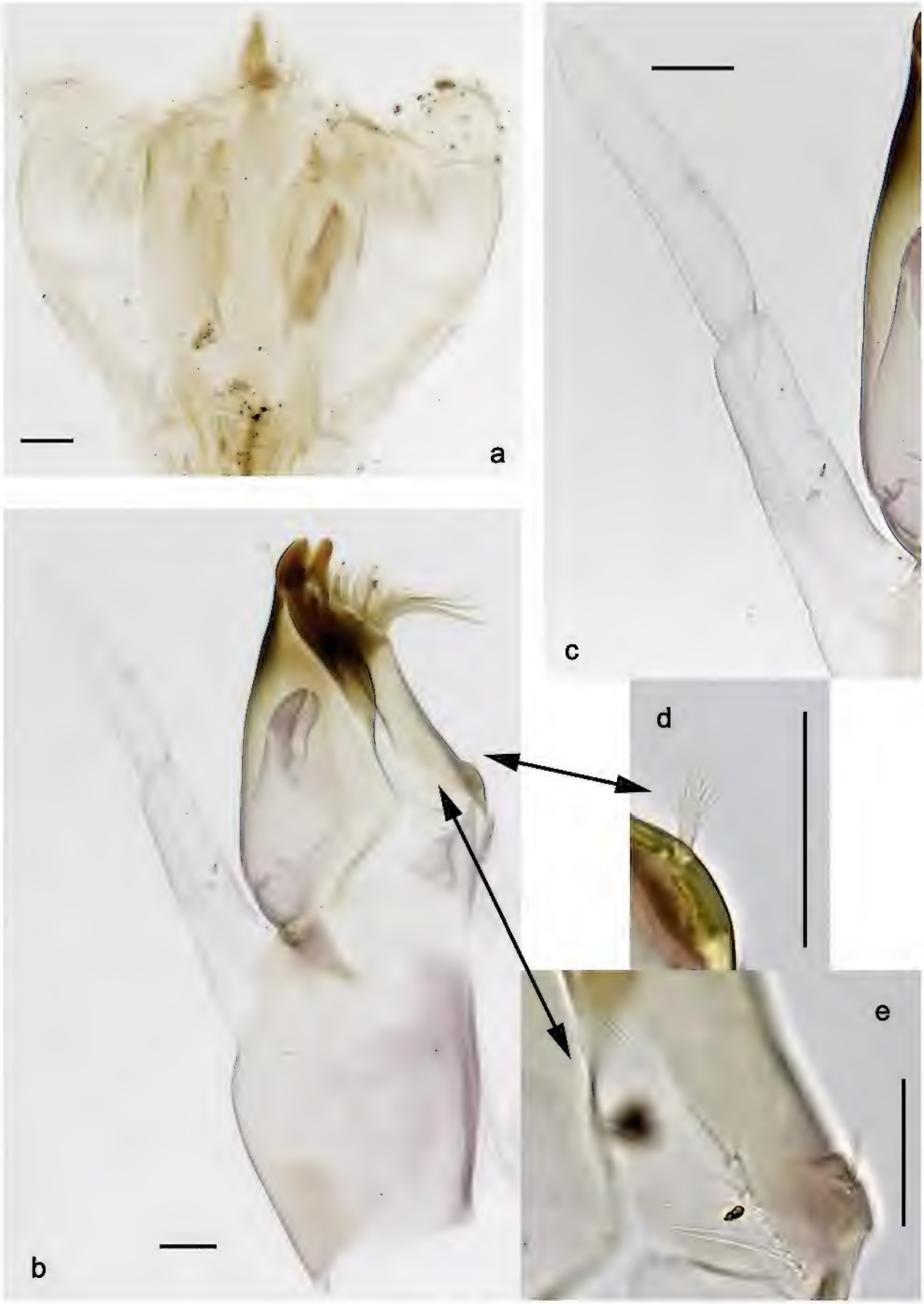

Figure 22. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d, e.** Sections of maxilla. Scale bars: 50 µm.

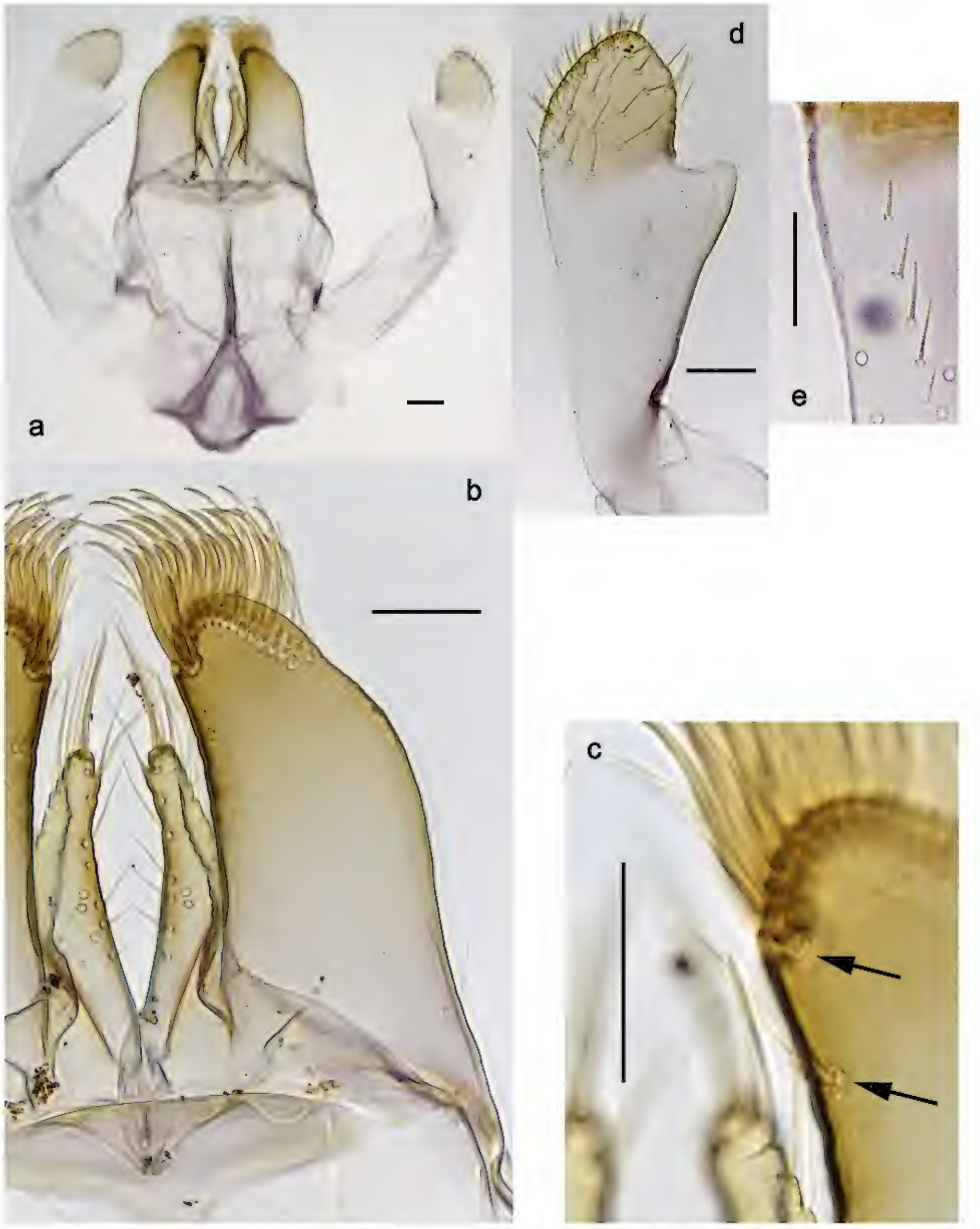

Figure 23. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Antenna (Fig. 25a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 21a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. eight long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 21c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with four denticles,

Figure 24. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tarsus, dorsal margin; **g.** Fore claw; **h.** Tip of fore claw. Scale bars: 50 µm.

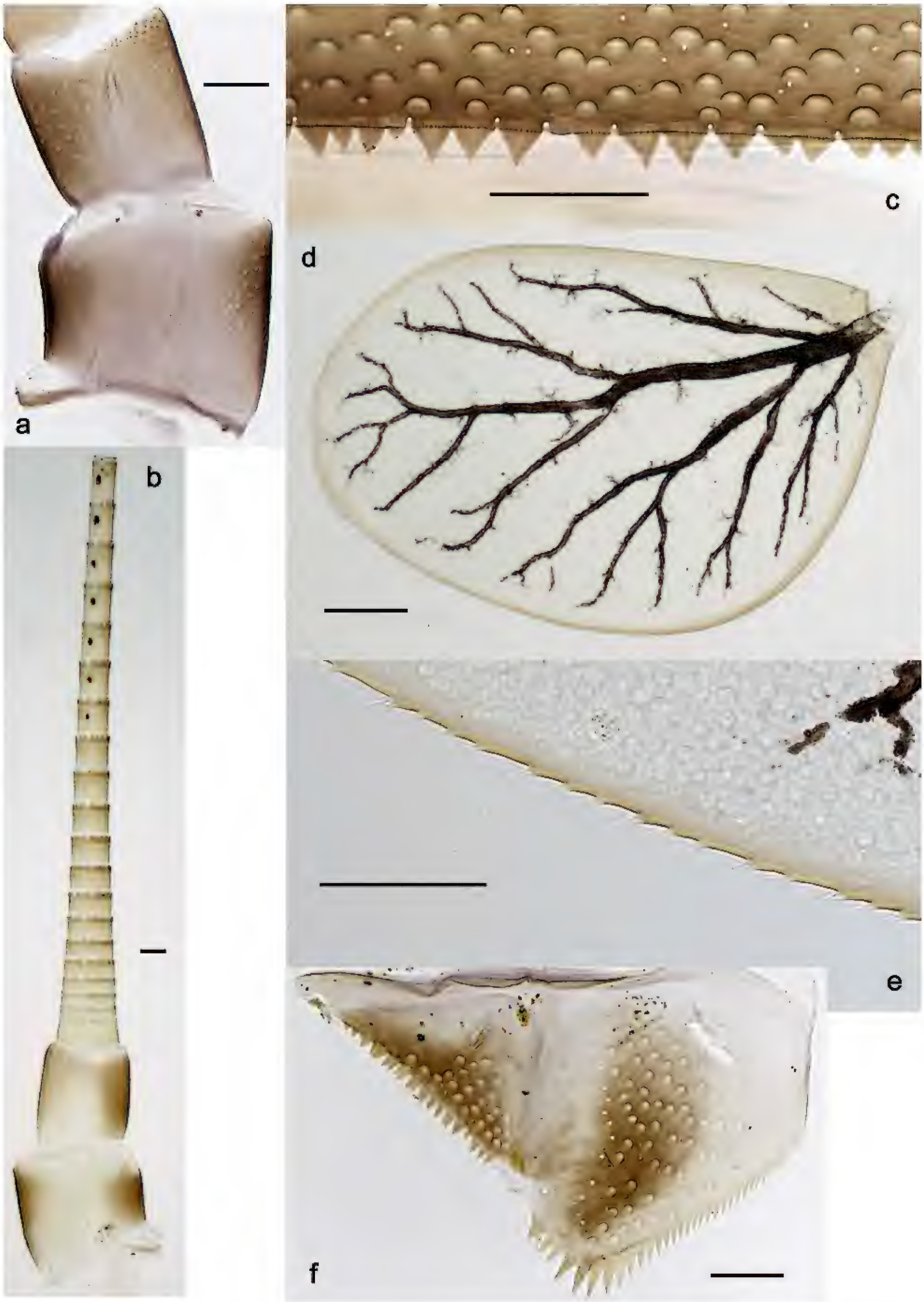

Figure 25. *Labiobaetis nabire* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, smooth, without denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 21e, f). Incisor and kinetodontium fused. Incisor with four denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, smooth, without denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 22a). Lingua longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 22b–e). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. eight long, simple setae. Maxillary palp approx. as long as length of galea-lacinia; 2-segmented; palp segment II approx. as long as segment I, and narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 23a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. seven spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; dorsally with two long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, distomedial protuberance; distal margin of protuberance slightly concave; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III oblong; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 24a–h). Ratio of foreleg segments 1.3:1.0:0.6:0.2. ***Femur.*** Fore femur length ca. 2.5× maximum width, middle and hind femur slightly less wide. Dorsal margin with row of ca. 25 short to medium, curved, spine-like, apically rounded setae; length of setae 0.13× maximum width of femur. Apex rounded, with many short, stout, apically rounded setae. Apex on posterior side with short, stout, apically rounded setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch rudimentary on fore and middle leg, reduced on hind leg. ***Tibia.*** Dorsal margin with row of short, stout, apically rounded setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface with very few stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with row of short, apically rounded setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. nine denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 25c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II–III with poorly developed spines; IV–V with triangular spines, mostly slightly wider than long; VI–IX with triangular spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 25d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V, VI and 1/3 VII combined. Tergalius VII as long as length of segments VIII and 1/3 IX combined.

Paraproct (Fig. 25f). Distally not expanded, with ca. 33 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the type locality in Nabire Regency, Central Papua Prov, Indonesia.

Distribution. Indonesia, Central Papua Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 774 m, together with *Labiobaetis papuaensis* Kaltenbach & Gattolliat, 2018.

Type material. ***Holotype.*** INDONESIA • larva; Papua Prov., Road Nabire-Enarotali KM 55; 03°29'48"S, 135°43'53"E; 774 m; 22.x.2011; leg. M. Balke; (PAP09); on slide; GBIFCH00980888; ZSM. ***Paratypes.*** INDONESIA • 11 larvae; same data as holotype; 3 on slides; GBIFCH00592568, GBIFCH00592569, GBIFCH00980889; MZL; 8 in alcohol; GBIFCH00975588, GBIFCH00975615; MZL.

9. *Labiobaetis simbuensis* sp. nov.

https://zoobank.org/B1E53880-E581-4F58-863F-32CA0910B01A

Figs 26–31, 38

Diagnosis. Larva. Following combination of characters differentiates *L. simbuensis* sp. nov. from other species of the group *petersorum*: A) labrum length 0.6× maximal width (Fig. 27a); B) both mandibles with row of minute denticles on margin between prostheca and mola (Fig. 27d, e, g h); C) labial palp segment II with small, thumb-like, hooked distomedial protuberance; segment III oblong (Fig. 29d); D) paraglossa dorsally with three long, spine-like setae near inner, distal margin (Fig. 29c);

Figure 26. *Labiobaetis simbuensis* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

E) tibia with row of short, spine-like setae on dorsal margin (Fig. 30a, e); posterior surface of tibia without scattered, stout setae; F) claw with ca. nine denticles (Fig. 30i); G) posterior margin of abdominal tergum IV with triangular or rounded spines, wider than long (Fig. 31c).

Description. Larva (Figs 26–31). Body length 4.7–6.1 mm. Caudalii: broken. Antenna: broken.

Cuticular colouration (Fig. 26a, b). Head, thorax and abdomen dorsally light brown. Head, thorax and abdomen ventrally beige. Legs light brown. Caudalii beige.

Hypodermal colouration. Antenna without dark brown dots on flagellum (Fig. 31b).

Antenna (Fig. 31a, b) with scape and pedicel sub-cylindrical, without distolateral process at scape.

Labrum (Fig. 27a, b). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of ca. seven long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 27c, d). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight, with row of minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 27f–i). Incisor and kinetodontium fused. Incisor with three denticles, outer denticle blade-like enlarged; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with row of minute denticles. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 28a). Lingua much longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally not expanded. Superlinguae distolaterally slightly protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 28b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of

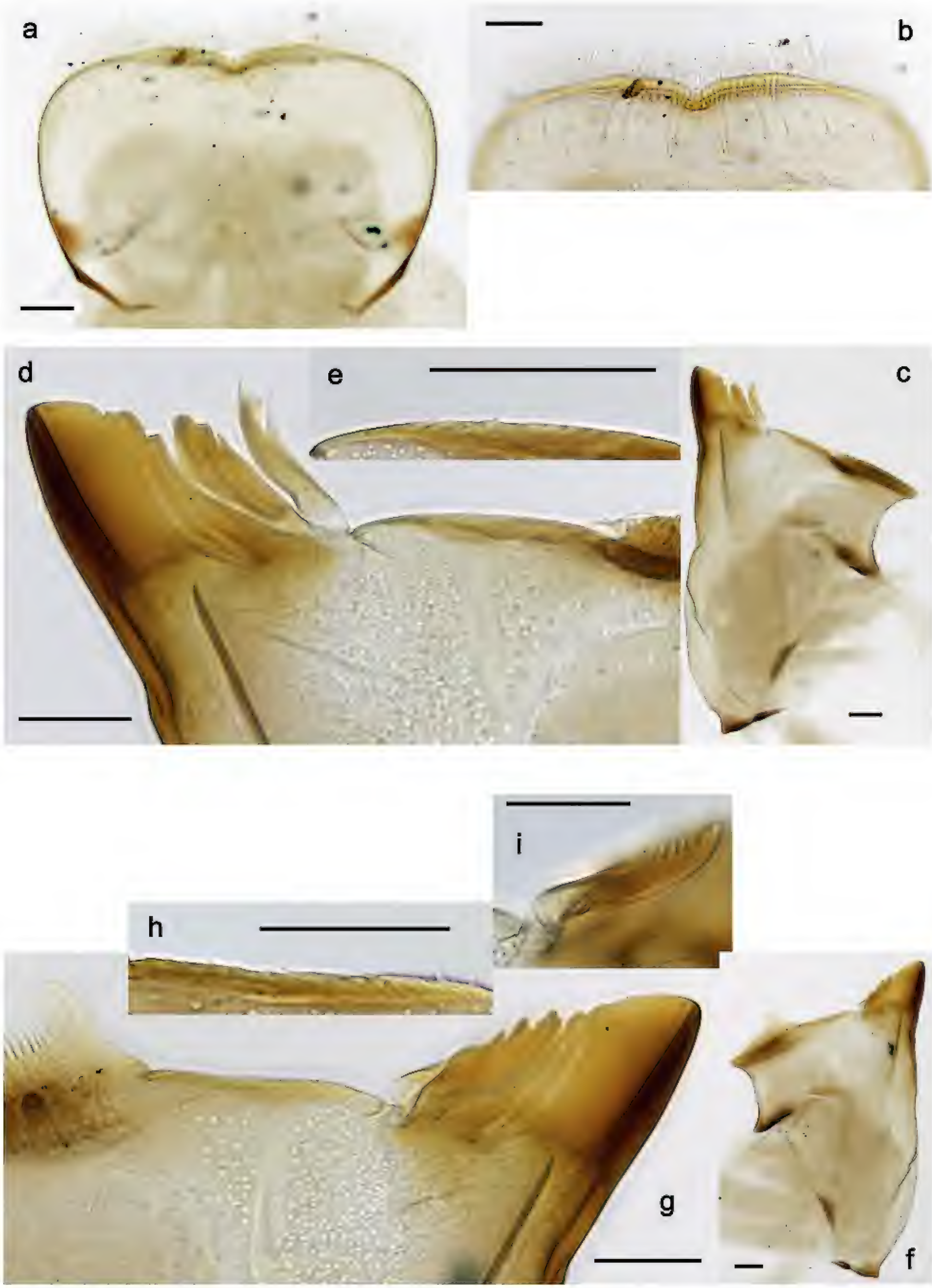

Figure 27. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Labrum; **b.** Section of labrum, dorsal focus; **c, d.** Right mandible; **e.** Right mandible, margin between prostheca and mola; **f, g.** Left mandible; **h.** Left mandible, margin between prostheca and mola; **i.** Left prostheca. Scale bars: 50 µm.

Figure 28. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

Figure 29. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Labium; **b.** Glossa and paraglossa, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

Figure 30. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, apex, posterior side; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tarsus, dorsal margin; **h.** Fore tarsus, ventral margin; **i.** Fore claw. Scale bars: 50 µm.

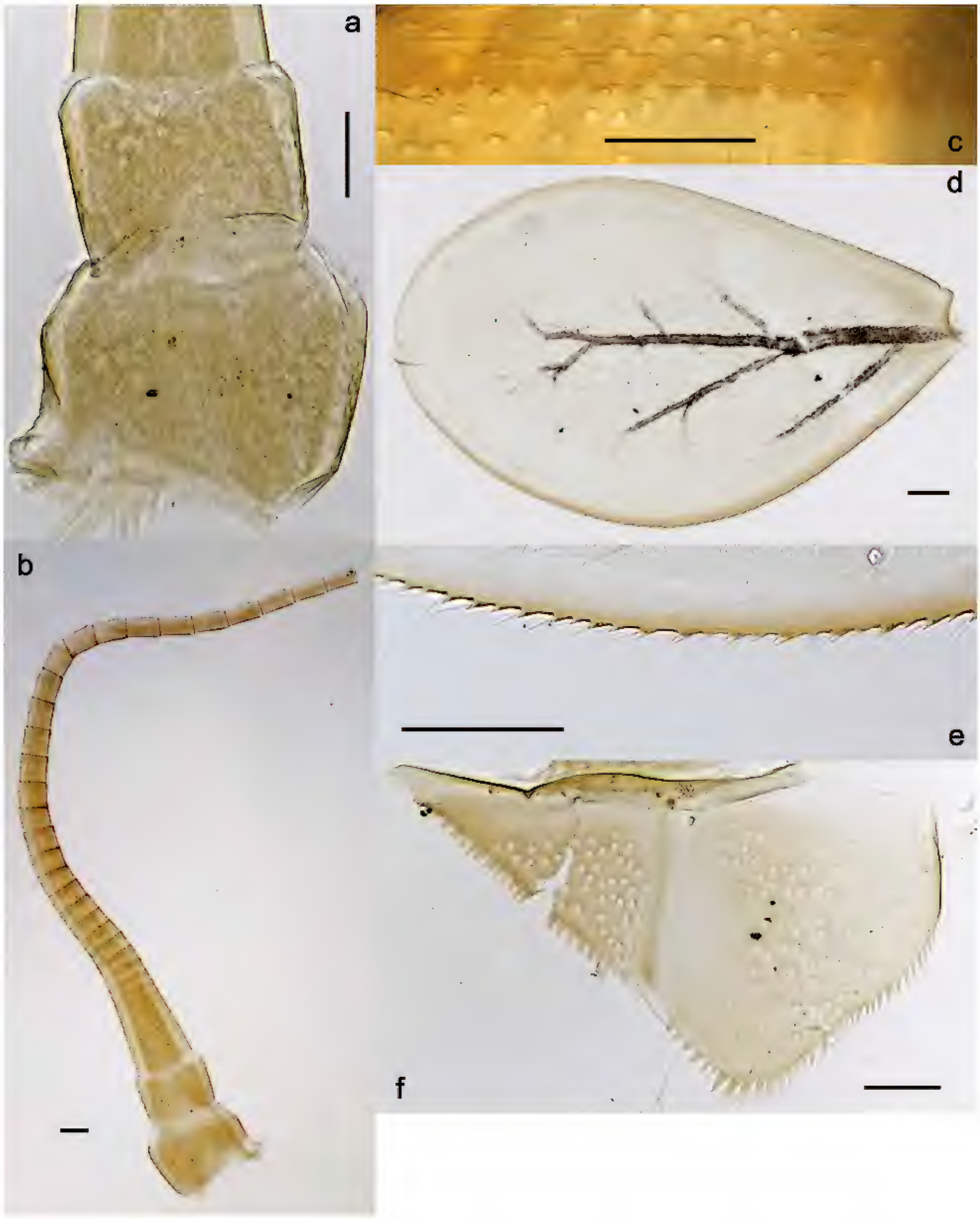

Figure 31. *Labiobaetis simbuensis* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Anal margin of tergalius IV; **f.** Paraproct. Scale bars: 50 µm.

setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. seven long, simple setae. Maxillary palp slightly longer than length of galea-lacinia; 2-segmented; palp segment II 1.5× as long as segment I, slightly narrower; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically pointed, constricted.

Labium (Fig. 29a–e). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with ca. eight spine-like seta; apex with three long, robust, apically pectinate setae; outer margin with ca. four spine-like setae; ventral surface with fine, simple, scat-

tered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; dorsally with three long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with small, thumb-like, hooked distomedial protuberance; distomedial protuberance 0.3× width of base of segment III; ventral surface with short, fine, simple setae; dorsally with row of ca. five spine-like setae near outer margin. Segment III oblong; length approx. width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Legs (Fig. 30a–i). Ratio of foreleg segments 1.5:1.0:0.6:0.2. ***Femur.*** Fore femur very wide, length ca. 2.2× maximum width, middle and hind femur less wide. Dorsal margin with row of ca. 26 long, curved, spine-like setae, and some short spine-like setae in between; length of setae 0.17× maximum width of femur. Apex rounded, with medium, spine-like, pointed setae. Apex on posterior side with short, stout, pointed setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; femoral patch absent on fore leg, rudimentary on middle leg and hind leg. ***Tibia.*** Dorsal margin with row of short, spine-like, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface without stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with one or few short, stout setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. nine denticles; distally pointed; with long, fine, transparent subapical seta on posterior side.

Abdominal terga (Fig. 31c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I–II smooth, without spines; III–V with triangular or rounded spines, wider than long; VI–IX with triangular spines, mostly wider than long.

Abdominal sterna. Unknown.

Tergalii (Fig. 31d, e). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Tracheae extending from main trunk to inner and outer margins. Tergalius IV as long as length of segments V, VI and 1/3 VII combined.

Paraproct (Fig. 31f). Distally not expanded, with ca. 35 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the type locality in Simbu Prov., Papua New Guinea.

Distribution. Papua New Guinea, Simbu Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 2350 m, together with *Labiobaetis wilhelmensis* Kaltenbach & Gattolliat, 2018 and *Labiobaetis gladius* Kaltenbach & Gattolliat, 2018.

Type material. ***Holotype.*** PAPUA NEW GUINEA • larva; Simbu Prov., Mt. Wilhelm, Pindaunde Creek, S5, oria. 6; 05°49'57"S, 145°06'08"E; 2350 m; 18.viii.1999; leg. L. Cizek; on slide; GBIFCH00592493; MZL. ***Paratype.*** PAPUA NEW GUINEA • 1 larva; same data as holotype; on slide; GBIFCH00975591; MZL.

Labiobaetis vitilis group of species

(diagnosis slightly enhanced from Kaltenbach and Gattolliat 2018)

Following combination of characters: A) antennal scape without distolateral process (Fig. 37a); B) labrum dorsally with submarginal arc of simple setae; C) maxillary palp without distolateral excavation (Fig. 34c); D) labial palp segment II with short thumb-like distomedial protuberance, segment III rather long (Fig. 35d); E) anterior surface of femur medially usually with stout setae (Fig. 36a, d); F) hind protoptera absent; G) tergalii present on abdominal segments II–VII.

The *L. vitilis* group is known from New Guinea only, including the following species:

Labiobaetis vitilis (Lugo-Ortiz & McCafferty, 1999)
Labiobaetis altus Kaltenbach & Gattolliat, 2018
Labiobaetis gindroi Kaltenbach & Gattolliat, 2018
Labiobaetis paravitilis Kaltenbach & Gattolliat, 2018
Labiobaetis wilhelmensis Kaltenbach & Gattolliat, 2018
Labiobaetis kokoda sp. nov.

10. *Labiobaetis kokoda* sp. nov.

https://zoobank.org/91E672B7-A49D-4490-9D3F-6A2B92FD41EA

Figs 32–38

Diagnosis. Larva. Following combination of characters differentiates *L. kokoda* sp. nov. from other species of *Labiobaetis*: A) labrum length 0.7× maximal width; dorsal submarginal arc of setae consisting of one plus 3–5 simple setae, 1st and 2nd setae after submedian seta closely together (Fig. 33a–c); B) incisor and kinetodontium of right mandible with four and three denticles; margin between prostheca and mola slightly convex, smooth (Fig. 33d, e); C) incisor and kinetodontium of left mandible with three and three denticles; margin between prostheca and mola almost straight, smooth (Fig. 33f, g); D) hypopharynx with well-developed medial tuft of stout setae (Fig. 34a); E) maxillary palp longer than galea-lacinia; segment II without distolateral excavation, apically pointed, constricted (Fig. 34b, c); F) labial palp segment II with thumb-like, distomedial protuberance; segment III oblong (Fig. 35a, d); G) femur dorsally with row of ca. 12 long, spine-like setae on margin; several such setae additionally in partial 2nd row near margin (Fig. 36a, b); H) claw with ca. 14 denticles (Fig. 36i); I) posterior margin of abdominal tergum IV with triangular or rounded spines, wider than long (Fig. 37c); J) antennal scape without distolateral process (Fig. 37a).

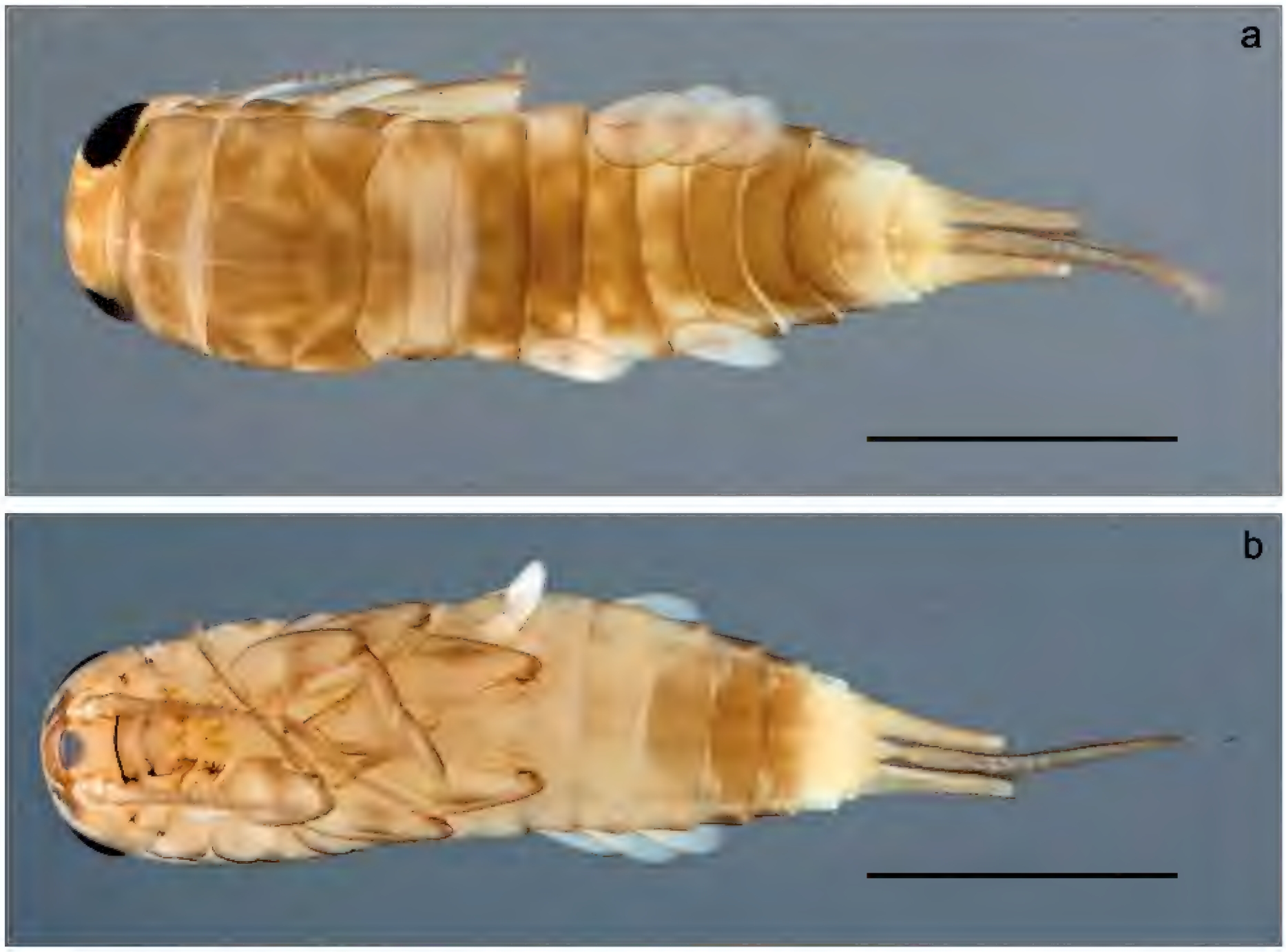

Figure 32. *Labiobaetis kokoda* sp. nov., larva habitus: **a.** Dorsal view; **b.** Ventral view. Scale bars 1 mm.

Description. Larva (Figs 32–37). Body length ca. 3 mm (immature). Cerci: broken. Paracercus ca. 0.4× body length. Antenna ca. 2.5× head length.

Cuticular colouration (Fig. 32a, b). Antenna light brown, darker at distal margins of segments. Head, thorax and abdomen dorsally brown, with pattern as in Fig. 32a; abdominal terga I, V and IX–X brighter. Head, thorax and abdomen ventrally light brown; abdominal sterna VI–VIII darker, IX–X brighter. Legs light brown, darker along dorsal margins of tibia and tarsus, femur medially and apically darker. Caudalii light brown.

Antenna (Fig. 37a) with scape and pedicel sub-cylindrical, without distolateral process at scape. Pedicel distally with triangular scales.

Labrum (Fig. 33a–c). Sub-rectangular, length 0.7× maximum width. Distal margin with deep medial emargination and small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of 3–5 long, simple setae, 1st and 2nd seta after submedian seta closely together. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae.

Right mandible (Fig. 33d, e). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles, inner margin of innermost denticle with row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola slightly convex, smooth. Tuft of setae at apex of mola present.

Left mandible (Fig. 33f, g). Incisor and kinetodontium fused. Incisor with three denticles; kinetodontium with three denticles. Prostheca robust, apicolaterally with small denticles and comb-shaped structure. Margin between prostheca and mola almost straight, smooth. Subtriangular process above level of area between prostheca and mola. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight.

Hypopharynx and superlinguae (Fig. 34a). Lingua slightly longer than superlinguae. Lingua longer than broad; medial tuft of stout setae well developed, distolaterally with two additional tufts of setae; distal half laterally slightly expanded. Superlinguae distolaterally slightly protruding; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 34b–d). Galea-lacinia ventrally with two simple, apical setae below canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one feathered spine-like seta and ca. six long, simple setae. Maxillary palp ca. 1.1× length of galea-lacinia; 2-segmented; palp segment II subequal in length to segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without distolateral excavation, apically slightly pointed, constricted.

Figure 33. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Labrum; **b, c.** Sections of labrum, dorsal focus; **d, e.** Right mandible; **f, g.** Left mandible. Scale bars: 50 µm.

Labium (Fig. 35a–e). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with ca. six spine-like seta; apex with two long and one medium robust, apically pectinate setae; outer margin with ca. six spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area; ventrally ca. four medium, fine, simple setae in anteromedial area; dorsally with five long, spine-like setae near inner margin. Labial palp with segment I approx. as long as length of segments II and III combined. Segment II with thumb-like, distomedial protuberance; distomedial protuberance 0.4× width of base of segment III; ventral surface with

Figure 34. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Hypopharynx and superlinguae; **b.** Maxilla; **c.** Maxillary palp; **d.** Section of maxilla. Scale bars: 50 µm.

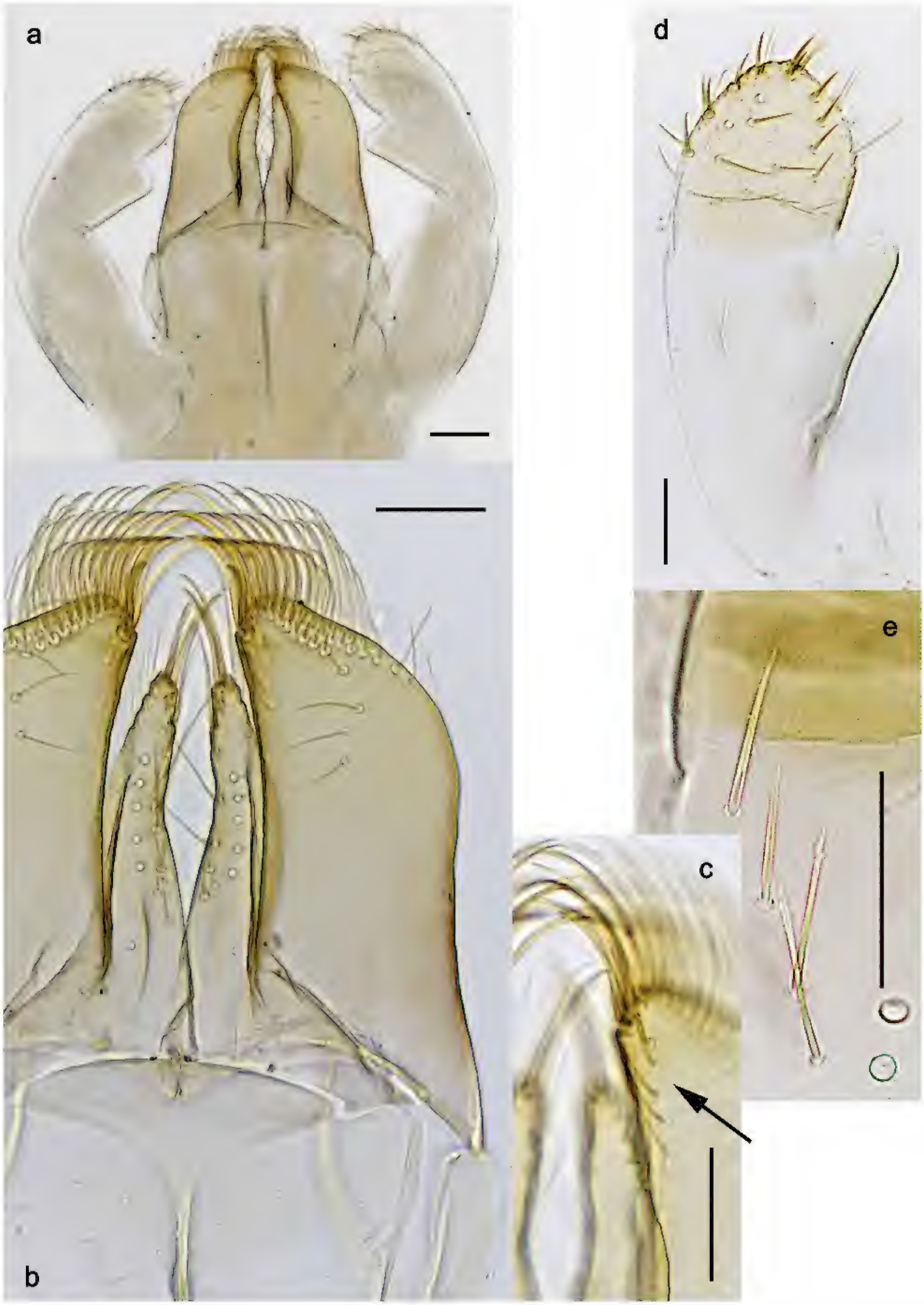

Figure 35. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Labium; **b.** Glossa, paraglossa and mentum, ventral focus; **c.** Section of paraglossa, dorsal focus; **d.** Labial palp, ventral focus; **e.** Section of labial palp, dorsal focus. Scale bar: 50 µm.

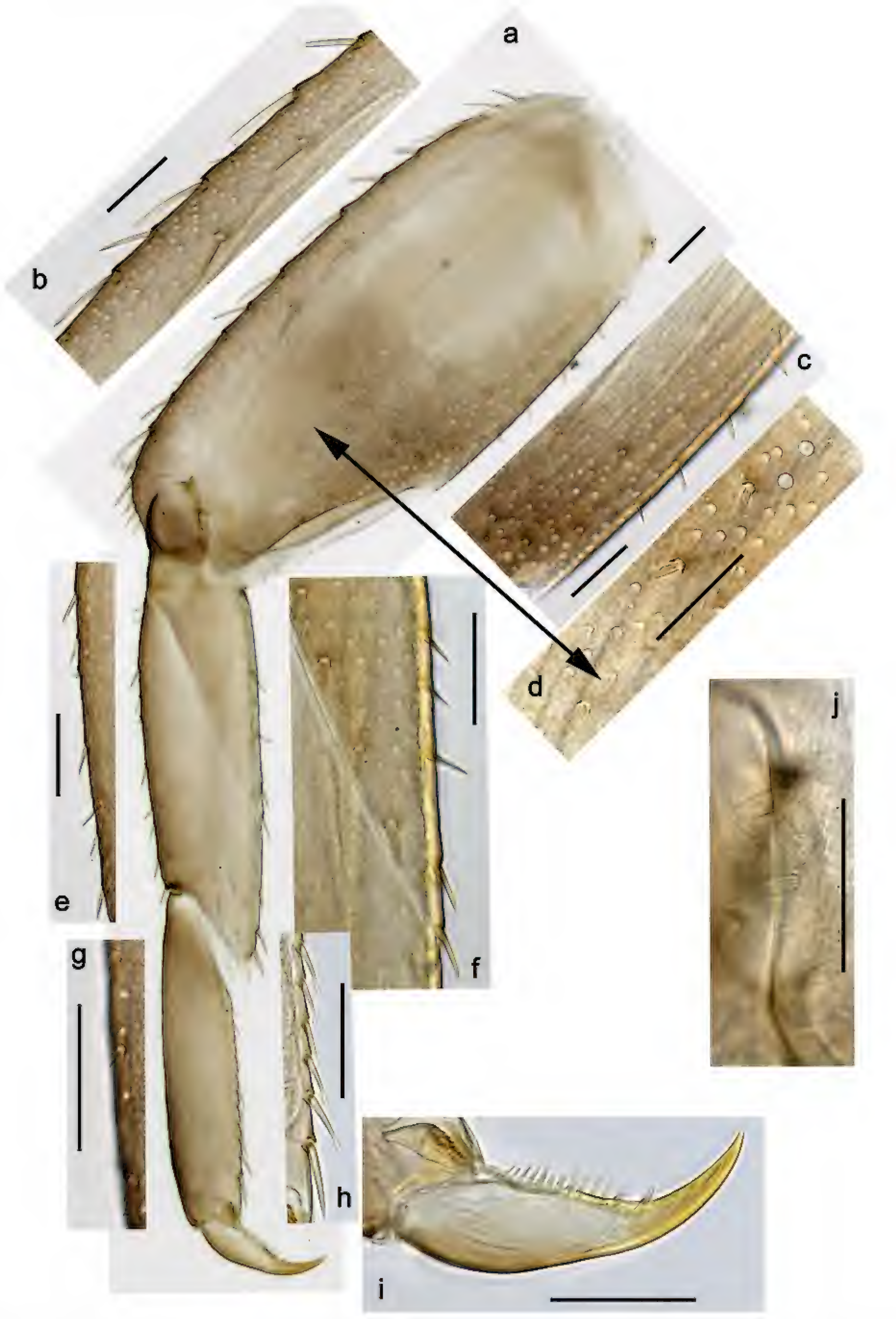

Figure 36. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Fore leg; **b.** Fore femur, dorsal margin; **c.** Fore femur, ventral margin; **d.** Fore femur, setae on distomedial surface; **e.** Fore tibia, dorsal margin; **f.** Fore tibia, ventral margin; **g.** Fore tarsus, dorsal margin; **h.** Fore tarsus, ventral margin; **i.** Fore claw; **j.** Fore femur, apex, posterior side. Scale bars: 50 µm.

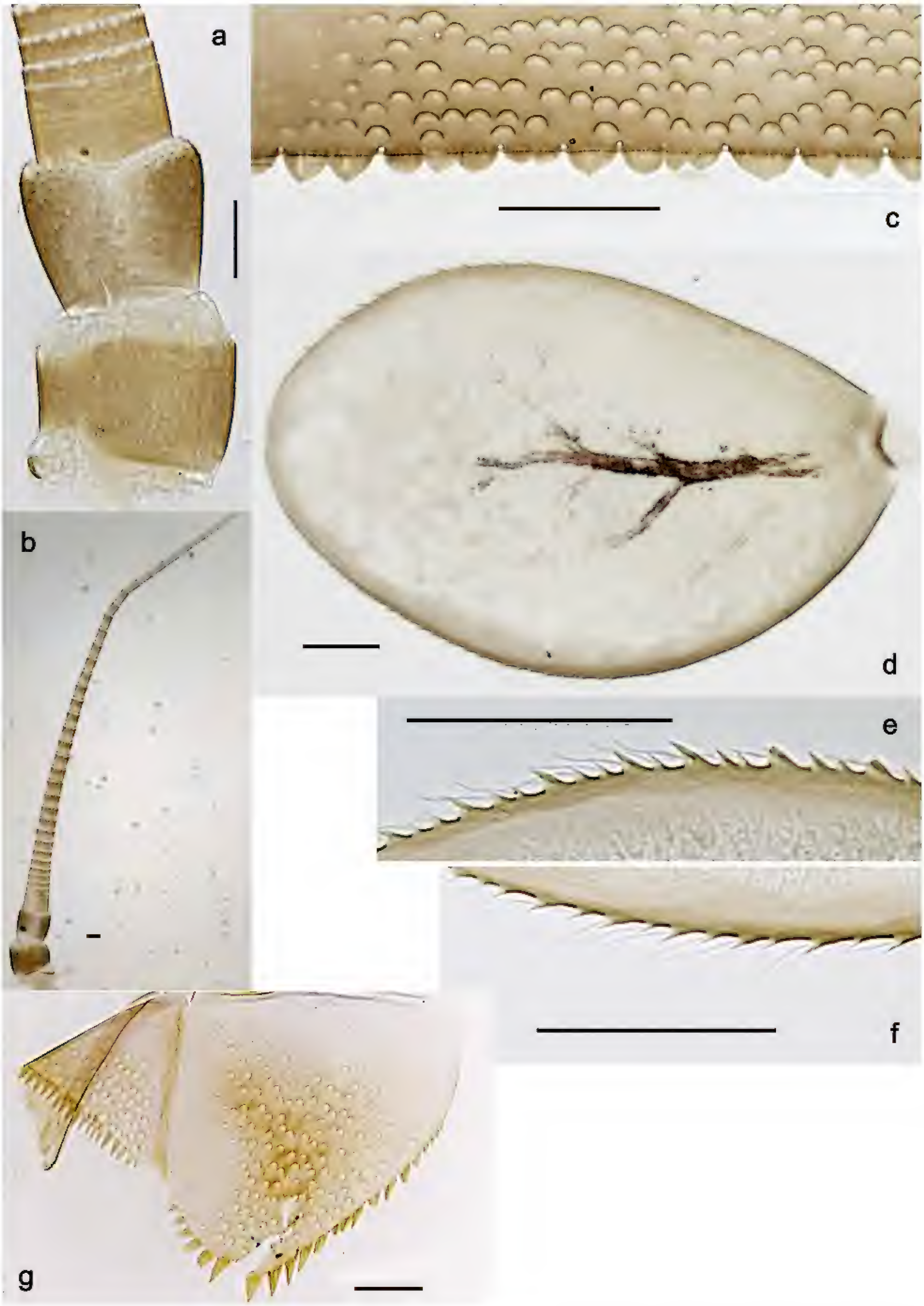

Figure 37. *Labiobaetis kokoda* sp. nov., larva morphology: **a.** Base of antenna; **b.** Antenna; **c.** Abdominal tergum IV; **d.** Tergalius IV; **e.** Costal margin of tergalius IV; **f.** Anal margin of tergalius IV; **g.** Paraproct. Scale bars: 50 µm.

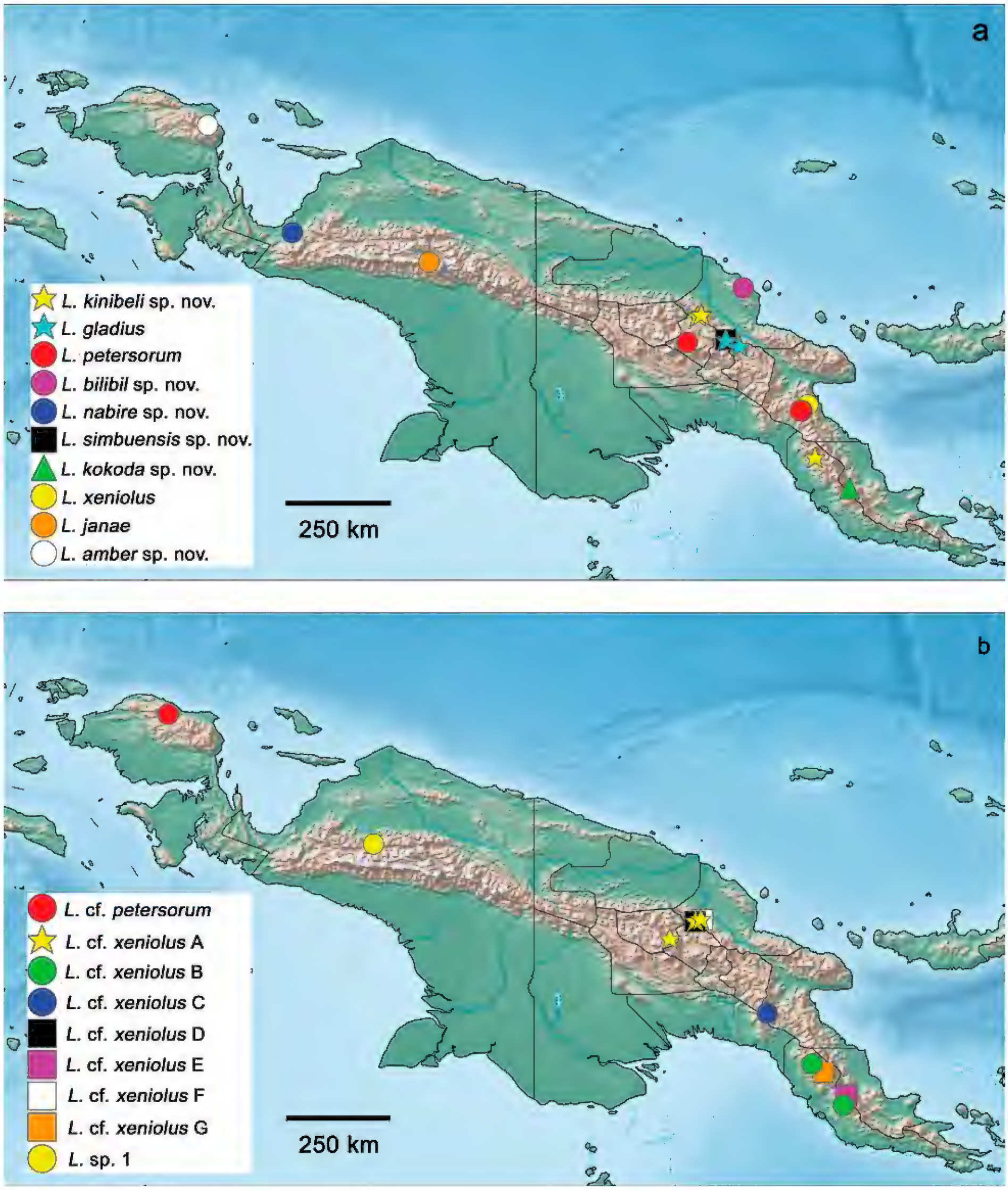

Figure 38. Distribution of species treated in this study: **a.** Species of group *petersorum* and *L. kokoda* sp. nov.; **b.** MOTUs of group *petersorum*, not described in this study.

short, fine, simple setae; dorsally with row of ca. four spine-like setae near outer margin. Segment III oblong; length ca. 1.1× width; ventrally covered with short to medium, spine-like, simple setae and short, fine, simple setae. Mentum ventrally with medium fine, simple setae scattered on distal part of surface.

Hind protoptera absent.

Legs (Fig. 36a–j). Ratio of foreleg segments 1.5:1.0:0.8:0.3. ***Femur.*** Femur very wide, length ca. 2.3× maximum width. Dorsal margin with row of ca. 12 long, curved, spine-like setae, and some additional spine-like setae in partial 2nd row near margin; length of setae 0.2× maximum width of femur. Apex rounded, with a pair of long, spine-like setae and several medium, spine-like setae. Apex on posterior side with few short, stout, setae on fore and middle leg, absent on hind leg. Stout, lanceolate, pointed setae scattered along ventral margin; several of such setae on distomedial surface. Femoral patch

rudimentary on fore and middle legs, reduced on hind leg. ***Tibia.*** Dorsal margin with row of short, spine-like, pointed setae. Ventral margin with row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Anterior surface with short, stout, lanceolate, pointed setae along patellatibial suture. Posterior surface without stout setae. Patellatibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with few short, stout setae. Ventral margin with row of curved, spine-like setae increasing in length distally. Claw with one row of ca. 14 denticles; distally pointed; without subapical seta on.

Abdominal terga (Fig. 37c). Surface with irregular rows of U-shaped scale bases. Posterior margin of terga: I smooth, without spines; II with rounded spines, much wider than long; III–VI with triangular or rounded spines, wider than long; VII–IX with triangular spines, longer than wide.

Abdominal sterna. Posterior margin of sterna: I–VI smooth, without spines; VII–IX with small, triangular spines.

Tergalii (Fig. 37d–f). Present on segments II–VII. Margin with small denticles intercalating fine, simple setae. Anal margin with both short and long, fine setae. Costal margin with alternating larger and smaller denticles. Tracheae not reaching inner and outer margins. Tergalius IV as long as length of segments V and VI combined.

Paraproct (Fig. 31f). Distally slightly expanded, with ca. 22 stout, marginal spines. Surface scattered with U-shaped scale bases. Cercotractor with numerous small, marginal spines.

Etymology. Referring to the Kokoda Trek in Central Prov. of Papua New Guinea, along which the specimens were collected.

Distribution. Papua New Guinea, Central Prov. (Fig. 38a).

Biological aspects. The specimens were collected at an altitude of 1390 m, together with *Labiobaetis lobatus* Kaltenbach & Gattolliat, 2018 and other species of *Labiobaetis*.

Type material. ***Holotype.*** PAPUA NEW GUINEA • larva; Central Prov., Kokoda Trek; 09°00'20"S, 147°44'15"E; 1390 m; i.2008; leg. Posman; (PNG 173); on slide; GBIFCH00975629; ZSM. ***Paratypes.*** PAPUA NEW GUINEA • 2 larvae; same data as holotype; on slides; GBIFCH00592683, GBIFCH00592684; MZL.

Genetics

The COI data set was >99.5% complete and included 36% of parsimony informative sites. The missing data almost exclusively resulted from a single sequence (GBIFCH00465182) that lacked 5' end. Pairwise COI distances across all sequences ranged from 0 to 23.3%. The overall mean p-distance within MOTUs was 1.4% (mean range 0–3.9%), and the overall mean p-distance between MOTUs was 18.7% (mean range 8.6%–23.2%). The maximum p-distance within all MOTUs ranged from 0 (*L. kinibeli* sp. nov.) to 5.5% (*L.* cf. *xeniolus* A), whereas it ranged from 0 (*L. kinibeli* sp. nov.) to 0.2% (*L. nabire* sp. nov.) when only considering newly described species. The minimum distance between all MOTUs ranged from 8.5% (*L. nabire* sp. nov.–*L.* sp. 1) to 23.2% (*L. janae*–*L.* cf. *xeniolus* E), whereas it ranged from 16.1% (*L. kinibeli* sp. nov.–*L. nabire* sp. nov.) to 21.7% (*L. amber* sp. nov.–*L. nabire* sp. nov.) when only considering newly described species. The four sequences of *L. kinibeli* sp. nov. were grouped in a well-supported monophyletic clade, supported as distinct MOTU in the ASAP, PTP and GMYC species delimitation analyses (Fig. 39). Similarly, the two sequences of *L. nabire* sp. nov. were grouped in a well-supported monophyletic clade, supported as distinct MOTU in all species delimitation analyses. *Labiobaetis amber* sp. nov., *L. bilibil* sp. nov. and *L. kokoda* sp. nov., each represented by a single COI sequence, were also supported as distinct MOTUs in all analyses. The three species delimitation methods were also congruent for the other MOTUs, except for *L.* cf. *xeniolus* A and B that were each split into 2 MOTUs according to ASAP and PTP (*L.* cf. *xeniolus* A) or PTP (*L.* cf. *xeniolus* B) methods.

Key to the species of the *Labiobaetis petersorum* group (larvae)

1 Labial palp segment III very short, conical (0.2×–0.3× length of segment II); paraproct with poorly developed marginal spines (Lugo-Ortiz et al. 1999: figs 109, 115) ..... *L. xeniolus*
– Labial palp segment III longer (at least 0.4×, usually 0.6× length of segment II) (Figs 4d); paraproct with marginal spines normally developed (Fig. 6f) 2
2 Paraproct with obvious expansion of distal margin (Kaltenbach and Gattolliat 2018: fig. 20e) ..... *L. janae*
– Paraproct without expansion of distal margin (Fig. 6f) 3
3 Dorsal margin of femur with ca. 25 spine-like setae (Fig. 24a) 4
– Dorsal margin of femur with ca. 37 to >50 spine-like setae (Fig. 12a) 5
4 Dorsal margin of femur with short to medium, spine-like setae (Fig. 24a, b); femur with medial, orange-brown spot on posterior side (Fig. 20a); tibia dorsal margin with row of short, apically rounded setae (Fig. 24e)..... *L. nabire* sp. nov.
– Dorsal margin of femur with long, spine-like setae (Fig. 30a, b); femur without orange-brown spot (Fig. 26a); tibia dorsal margin with row of medium pointed setae (Fig. 30e) ..... *L. simbuensis* sp. nov.
5 Labrum very wide (length 0.5× width) (Fig. 9a); labial palp segment II with elongate, slightly hooked, distomedial protuberance (Fig. 11c); posterior margin of abdominal tergum IV with triangular, sharply pointed spines, longer than wide (Fig. 13c) ..... *L. bilibil* sp. nov.
– Not this combination of characters 6

6 Tibia dorsal margin with two rows of short, stout setae (Fig. 18e); margin between prostheca and mola of both mandibles with minute denticles, subtriangular process with minute denticles at base (Fig. 15e, h, i); posterior margin of abdominal tergum IV with triangular spines, slightly wider than long (Fig. 19c) ..... *L. kinibeli* sp. nov.
– Not this combination of characters 7
7 Labial palp segment III rather short (0.4× length of segment II) (Fig. 4d); posterior margin of abdominal tergum IV with triangular spines, slightly wider than long (6c) ..... *L. amber* sp. nov.
– Labial palp segment III long (0.6× length of segment II) (Kaltenbach and Gattolliat 2018: fig. 17h); spines at posterior margin of abdominal tergum IV of different shape 8
8 Labial palp segment III oblong, segment II with broad, thumb-like protuberance; posterior margin of abdominal tergum IV with rounded spines, wider than long (Kaltenbach and Gattolliat 2018: figs 17h, 18c) ..... *L. gladius*
– Labial palp segment III slightly pentagonal, segment II with rather small, thumb-like protuberance, distal margin of protuberance slightly concave; posterior margin of abdominal tergum IV with triangular, pointed spines, longer than wide (Kaltenbach and Gattolliat 2018: fig. 16c, d) ..... *L. petersorum*

Table 2. GPS coordinates of locations of examined specimens.

Species	Country	Location	Coordinates
L. petersorum	Papua New Guinea	Morobe Prov.	07°20'14"S, 146°42'57"E
			07°20'05"S, 146°41'05"E
			05°51'29"S, 144°14'35"E
L. xeniolus	Papua New Guinea	Morobe Prov.	07°12'28"S, 146°50'41"E
L. gladius	Papua New Guinea	Simbu Prov.	05°49'58"S, 145°06'08"E
			05°48'03"S, 145°04'09"E
			05°49'02"S, 145°05'16"E
		Western Highlands Prov.	05°15'52"S, 144°32'43"E
		Easterm Highlands Prov.	05°56'48"S, 145°22'14"E
L. janae	Indonesia	Papua Prov.	04°07'46"S, 138°40'46"E
L. amber sp. nov.	Indonesia	Papua Barat Prov.	01°10'59"S, 133°54'44"E
L. bilibil sp. nov.	Papua New Guinea	Madang Prov.	04°41'01"S, 145°26'55'E
L. kinibeli sp. nov.	Papua New Guinea	Central Prov.	08°20'31"S, 146°59'49"E
		Western Highlands Prov.	05°17'14"S, 144°28'13"E
		Western Highlands Prov.	05°15'10"S, 144°32'49"E
		Western Highlands Prov.	05°15'52"S, 144°32'43"E
L. nabire sp. nov.	Indonesia	Papua Prov.	03°29'48"S, 135°43'53"E
L. simbuensis sp. nov.	Papua New Guinea	Simbu Prov.	05°48'03"S, 145°04'09"E
L. cf. *petersorum*	Indonesia	Papua Barat Prov.	00°47'02"S, 133°04'20"E
L. cf. *xeniolus* A	Papua New Guinea	Enga Prov.	05°38'06"S, 143°55'20"E
		Western Highlands Prov.	05°14'50"S, 144°28'27"E
		Madang Prov.	05°12'42"S, 144°35'31"E
L. cf. *xeniolus* B	Papua New Guinea	Central Prov.	08°20'31"S, 146°59'49"E
		Central Prov.	09°14'20"S, 147°40'32"E
L. cf. *xeniolus* C	Papua New Guinea	Morobe Prov.	07°14'49"S, 146°01'20"E
L. cf. *xeniolus* D	Papua New Guinea	Western Highlands Prov.	05°16'06"S, 144°27'52"E
L. cf. *xeniolus* E	Papua New Guinea	Central Prov.	09°01'57"S, 147°44'27"E
L. cf. *xeniolus* F	Papua New Guinea	Madang Prov.	05°13'23"S, 144°37'17"E
		Madang Prov.	05°13'20"S, 144°37'37"E
L. cf. *xeniolus* G	Papua New Guinea	Central Prov.	08°31'35"S, 147°14'06"E
L. sp. 1	Indonesia	Papua Prov.	03°35'17"S, 137°30'41"E
L. kokoda sp. nov.	Papua New Guinea	Central Prov.	09°00'20"S, 147°44'15"E

Discussion

Assignment to *Labiobaetis*

For the assignment of the new species to *Labiobaetis* we refer to Kluge and Novikova (2014), Müller-Liebenau (1984) and McCafferty and Waltz (1995). *Labiobaetis* is characterized by a number of characters, some of which are not found in other taxa (Kluge and Novikova 2014): antennal scape sometimes with a distolateral process (Kaltenbach et al. 2020: fig. 2h); maxillary palp two segmented with excavation at inner distolateral margin of segment II, excavation may be poorly developed or absent (Kaltenbach et al. 2020: fig. 2n–p); labium with paraglossae widened and glossae diminished; labial palp segment II with distomedial protuberance (Fig. 4d). All these characters vary and may be secondarily lost (Kluge and Novikova 2014). The concept of *Labiobaetis* is also based on additional characters, summarized and discussed in Kaltenbach and Gattolliat (2018, 2019).

Labiobaetis petersorum group

The morphological groups within *Labiobaetis* are primarily a working tool, but could also serve as a basis for

future studies on the generic delimitation and phylogeny of this genus. The inclusion of nuclear gene sequences may prove that some are natural groups.

Five of the new species, *L. amber* sp. nov., *L. bilibil* sp. nov., *L. kinibeli* sp. nov., *L. nabire* sp. nov. and *L. simbuensis* sp. nov., belong to the group *petersorum* as originally defined in Kaltenbach and Gattolliat 2018: incisor of both mandibles with outermost denticle blade-like enlarged (Fig. 9d, g; in worn condition as Fig. 2d, f); labrum dorsally with submarginal arc of long, simple setae (Fig. 2b); labial palp segment II with rather short, rounded distomedial protuberance (Fig. 4d). The investigation of the new species and re-examination of type material of known species allowed to enhance the morphological characterisation of the group *petersorum* (see above).

Subapical setae

Re-examination of type material of *L. gladius* and *L. janae* revealed the presence of a long, fine subapical setae on the claws, as it is usually the case in the group *petersorum*. They are not mentioned or figured in the original description. These subapical setae seem to break easily or to stick along the posterior side of the claw and therefore, may be difficult to see. The subapical setae of the group *petersorum* are inserted on posterior side of the claw, in anterior position (between distalmost denticle and tip of the claw). On anterior side, there is a short subapical seta (*L. amber* sp. nov.; Fig. 7). *Labiobaetis petersorum* seems to be an exception for this character, as subapical setae were originally not described or figured and were also not detected during an earlier re-examination of a paratype by the authors (without specifically looking for this character). Additionally, *L.* cf. *petersorum* from a very distant location compared to the type locality, which has all characters of *L. petersorum*, is also missing subapical setae. The original description of *L. xeniolus* does also not mention or figure subapical setae, nor were they discovered during a re-examination of two paratypes based on stacking videos of fore claws. Other legs were not embedded in these paratype slides. However, this study revealed several MOTUs with the same larval morphology than *L. xeniolus*, and they all have subapical setae.

Two other species of *Labiobaetis*, which are not part of the group *petersorum* are known to have subapical setae, *L. catadupa* Kaltenbach & Gattolliat, 2021 from Borneo and *L. toraja* Kaltenbach & Gattolliat, 2021 from Sulawesi (both are forming the group *catadupa*). In both cases, their position is as usually on posterior side, but in posterior position (at or close to the distalmost denticle; "posterior seta" according to Kluge and Novikova 2014: 11; Kaltenbach and Gattolliat 2021: fig. 4a, b).

One single, long subapical seta or one on each side of the claw were also described from other genera of Baetidae (see discussion and citations in Kaltenbach and Gattolliat 2021). The genus *Philibaetis* Kaltenbach & Gattolliat, 2021 has two or more subapical setae on posterior side of the claw, which also exists in a few other genera of Baetidae (see discussion and citations in Kaltenbach et al. 2021b).

Mandibles with blade-like incisors

The most obvious character present in all species of *Labiobaetis* group *petersorum* is the incisors with blade-like enlarged outermost denticles on both mandibles. This character was also observed in other genera of Baetidae, and is most probably a convergence: e.g. *Branchiobaetis* Kaltenbach, Kluge & Gattolliat, 2022; *Philibaetis* Kaltenbach & Gattolliat, 2021; Liebebiella Waltz & McCafferty, 1987; and *Baetis* Leach, 1815 (Müller-Liebenau 1982, 1984; Müller-Liebenau and Hubbard 1985; Kaltenbach et al 2021b, 2022b). Interestingly, this character is usually combined with a wide, sub-rectangular labrum with a well-developed, dorsal, submarginal arc of long, simple setae. It could be a co-adaptation of both characters to a specific way of alimentation like scraping (Sartori and Brittain 2015). Further studies are necessary to explore this possibility in the future. However, *Baetis collinus* Müller-Liebenau & Hubbard, 1985 is an exception with a rather narrow labrum (Müller-Liebenau and Hubbard 1985: fig. 4a, e).

Genetics

The five newly described species included in the genetic investigations are highly supported by our CO1-based analyses. The minimum p-distance between MOTUs of 8.5% (distance between *L. nabire* sp. nov. and *L.* sp. 1) is far beyond the generally accepted threshold of 3% divergence for mayflies (e.g., Ball et al. 2005; Kjærstad et al. 2012; Gattolliat et al. 2015), and all three species delimitation analyses are congruent and support their species status, despite a very limited intraspecies diversity. *L. bilibil* sp. nov. and *L.* cf. *petersorum* are supported as related to each other (Fig. 39) and the morphology is supporting this as well: both have long, sharply pointed spines at posterior margins of abdominal terga; similar setation of the legs; and a similar shape of labial palps segments II and III. The main differences are the shape of the labrum (length ca. 0.6× width in *L.* cf. *petersorum* and 0.5× in *L. bilibil* sp. nov.), the shape of the tarsus (slender in *L.* cf. *petersorum*, relativ short and wide in *L. bilibil* sp. nov.) and the subapical setae (absent in *L.* cf. *petersorum*, present in *L. bilibil* sp. nov.). Other relations are supported between *L. janae* and *L. kinibeli* sp. nov. and between *L. nabire* sp. nov. and *L.* sp.1 (Fig. 39). In the first case, the larval morphology is not showing further evidence, and in the second case, there are morphological similarities of *L.* sp. 1 with both *L. nabire* sp. nov. and *L. kinibeli* sp. nov. However, most species of the group *petersorum* are morphologically close and we are mostly lacking characters to recognise and support subgroups inside this group.

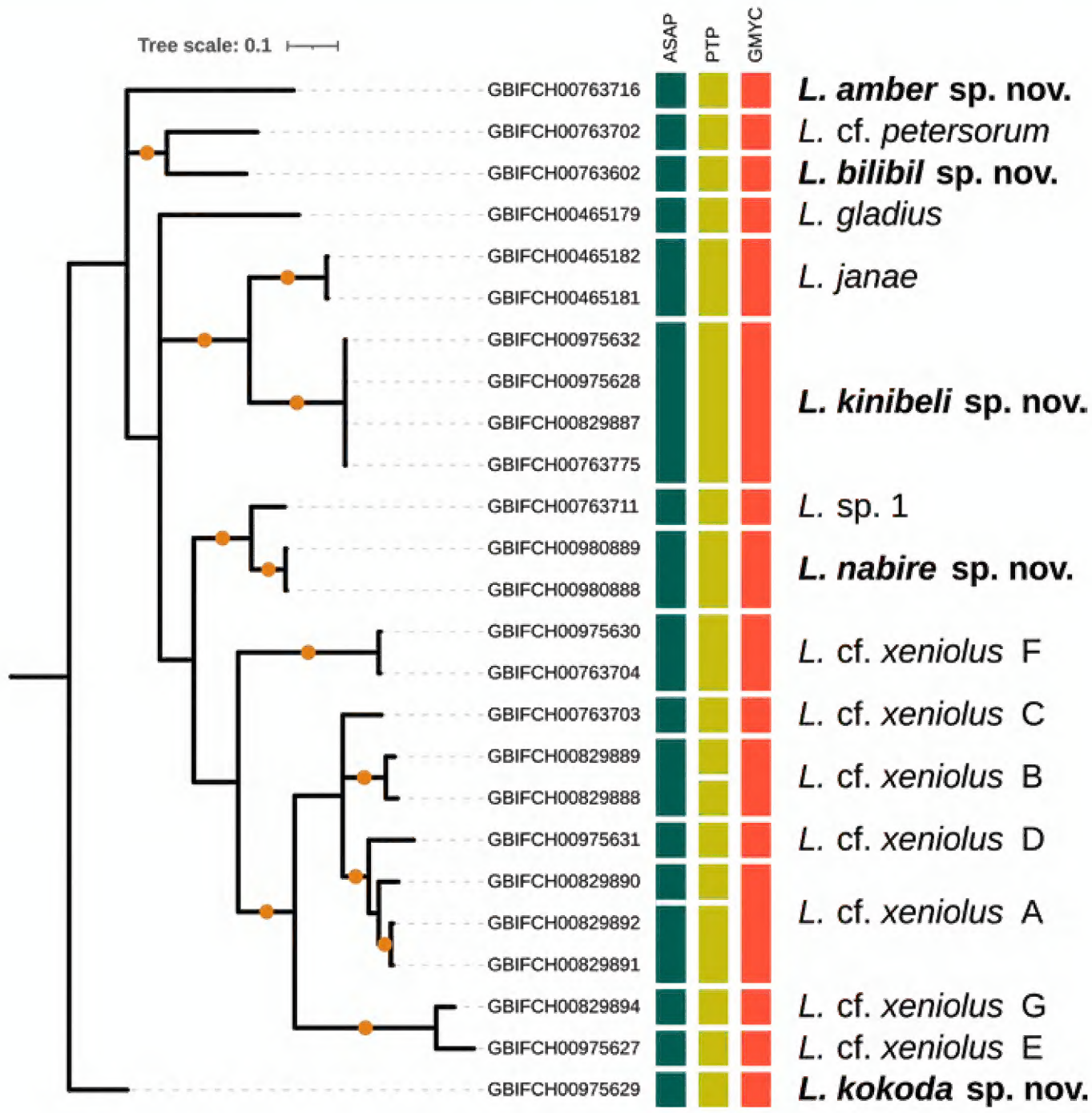

Figure 39. Bayesian majority-rule consensus tree reconstructed from the CO1 data set. Coloured vertical boxes indicate species delimitation hypothesis (MOTUs) according to the ASAP, PTP and GMYC methods. Tips are labelled according to Table 1. For each GMYC-based MOTU, the corresponding species name (where available) is provided, with newly described species specified in bold. Circles on branches indicate Bayesian posterior probabilities > 0.9.

Interestingly, the seven *L.* cf. *xeniolus* MOTUs are integrated in the same clade (although without a strong support), suggesting a potentially cryptic species complex that requires further investigation. We recommend that future studies include more populations to increase the amount of intraspecies diversity within the *L.* cf. *xeniolus* complex, as well as information from the nuclear genome to complement the classic COI-based approach.

Taking into account the extreme biodiversity in New Guinea, the rather poor collection activities in the past, with many still unexplored regions, and the obvious richness of *Labiobaetis* on this island, we have to expect many more new species with further collections in the future.

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